THE
AMERICAN NATURALIST

CHROMOSOME BEHAVIOR, INHERITANCE AND SEX DETERMINATION IN SCIARA[1]

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INTRODUCTION

THE present paper has been prepared in response to numerous requests for a general account of the genetic and cytological peculiarities of Sciara which will bring together the results published in various journals and will bring the evidence up to date. Such an account is especially needed because of the fact that in endeavoring to interpret our findings in Sciara in accordance with principles applying commonly to other organisms some misinterpretations were presented in our early papers. These could only be corrected as the extent of the divergence between Sciara and the more "typical" organisms gradually became clear. The investigations have been carried out not only to explore the extent of this divergence, but more especially because the peculiarities in Sciara serve to throw light on special subjects of general biological interest. Thus far the work has centered largely around problems concerning the nature and function of sex chromosomes, the distinction between soma and germ-line, the evolution of the genetic mechanism, embryonic differentiation (especially as it affects the chromosomes), the mechanism of mitosis and general aspects of chromosome behavior.

Much of the work was made possible by aid received

from the Committee for Research in Problems of Sex, National Research Council. Those engaged in it are indicated in the references cited. It should be emphasized that the studies are by no means complete and that numerous features, including sex determination itself, are not yet fully analyzed.

No attempt will be made here to treat in detail the features which are still obscure, or to include detailed data on any topics. Such material will be given in a more comprehensive paper to appear later. The present brief account is essentially a résumé in which the known facts are brought together, their interrelationships and general significance pointed out, and earlier misinterpretations corrected. Special emphasis is laid on the peculiar and complicated mechanism of sex determination, the production of unisexual families, the uniparental inheritance through the male, the peculiar "limited" chromosomes present in the germ-line but not in somatic tissues, and the precise elimination processes which remove certain chromosomes during embryonic development and others during spermatogenesis. Such phenomena show that we are dealing with a group of organisms in which wide and apparently fundamental modifications of the genetic mechanism have become established. In some respects these phenomena violate apparently well-established principles of chromosome behavior, and reveal what may be called a greater flexibility or wider range of potentiality in the genetic mechanism than had formerly been considered possible.

Taxonomic Relationships of Sciara

The genus Sciara belongs among the lower Diptera (two-winged flies). According to the classification of Johannsen (1912) which has been followed in the present work, it includes a large number of species and represents a group falling within, or closely related to, the Mycetophilidae or fungus gnats. Its exact relationships, however, seem obscure, and as some authors have intimated it may deserve family rank. The present investigation has not yet thrown any light on this subject.

The flies of this genus are practically all small, comparatively delicate and mostly black, although some range up to approximately half the size of a house fly, or larger, and in certain species the color ranges into olive and even yellow.   Not all species are suitable for laboratory study, but many are favorable for genetic work, and all those thus far investigated are favorable for cytological purposes.   Culture technique, etc., has been described elsewhere (Smith-Stocking, 1936).   The writer is greatly indebted to Professor O. A. Johannsen for his generous aid in identifying material and providing information concerning taxonomic relationships.

Fourteen or more species have been investigated in the present study, but most of the genetic work has been confined to four species, as will be indicated under the appropriate headings below.

Conditions in Sciara Contrasted with Those in "Typical" Organisms

Most of the peculiarities found in Sciara appear to be interdependent and need to be considered in relation to one another.   It is desirable, therefore, even at the expense of some repetition, to present a brief preliminary picture of the situation as a whole before trying to discuss the individual topics.   This is done in the following outline, which serves to contrast conditions in Sciara with those in "typical" organisms and will also serve as a summary for the paper.   The outline is necessarily brief and subject to some qualification in regard to details, as will appear in the later paragraphs.   It is based primarily on conditions in *S. coprophila* Lintner, the species best known genetically and cytologically.   For the most part, however, it applies also to the other species studied, except for the fact that some of the latter give modified bisexual, instead of "unisexual" families.   The diagrams presented in Figs. 1 and 2 may aid in interpreting the outline.
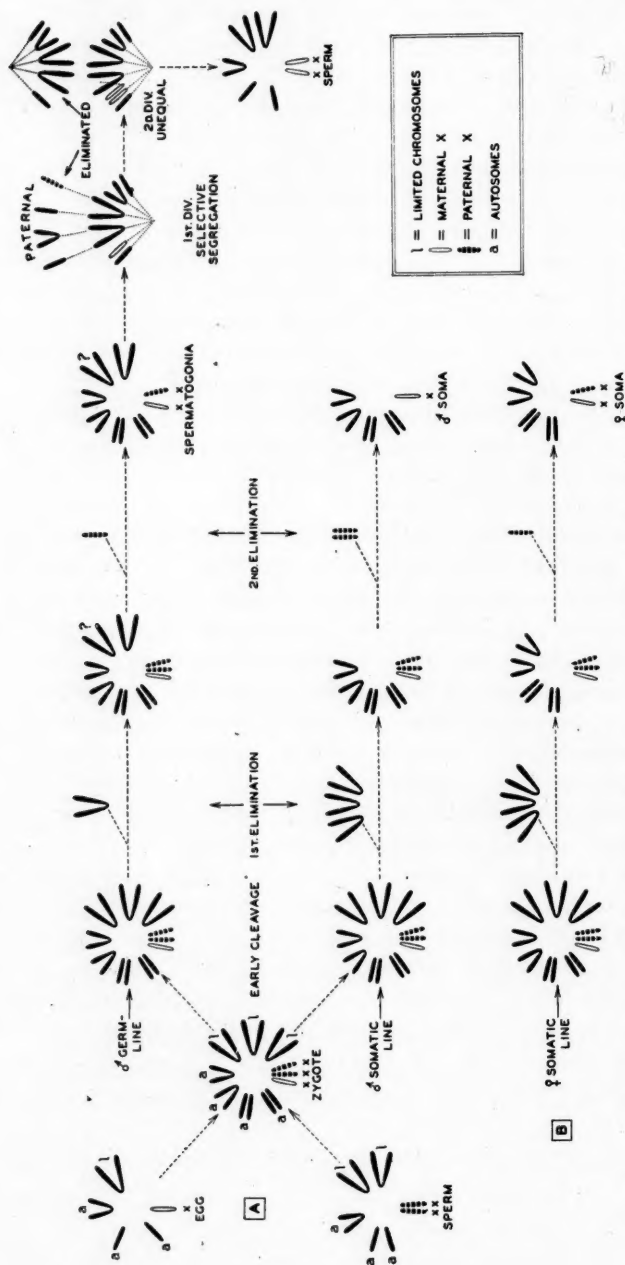
(1) *The chromosome group.*   In typical organisms

FIG. 1. A. Diagram illustrating the history of the chromosomes during development and gametogenesis in the male Sciara, using S. coprophila as an example. The maternal X chromosomes which go into the sperm become, of course, the paternal XX at fertilization. As noted in the text the number of "limited" chromosomes may vary from one to three. Diagram A serves equally well to represent conditions in the female except as regards gametogenesis, which follows the standard pattern, and as regards the second chromosome elimination from the soma, which removes only one paternal X as shown in diagram B. Diagram B applies to both male-producing and female-producing females; but in the latter, of course, the maternal sex chromosome would be designated X' instead of X.

each kind of chromosome—at least one member of each pair—is present in all tissues. In Sciara, however, except for two of the fourteen species thus far studied, one type of chromosome is limited to the germ-line, as indicated below, and is referred to as the "limited" chromosome. The basic chromosome group, therefore, contains three classes of chromosomes, ordinary autosomes, sex chromosomes and "limited" chromosomes.

(2) *Chromosome contributions of egg and sperm.* Instead of the egg and sperm contributing equivalent haploid sets of chromosomes, only the egg contributes a haploid set in Sciara (an X and 3 autosomes, with or without a "limited" chromosome). The sperm contributes two sister X chromosomes, and one or more "limited" chromosomes as well as the expected three autosomes. Fertilization is monospermic, not polyspermic as in many other insects (Schmuck and Metz, 1932).

(3) *Alteration of the chromosome group during embryonic development.* In typical organisms the fundamental chromosome group remains constant in all tissues during embryonic development. In Sciara the original chromosome group of the fertilized egg is maintained through only five or six cleavage divisions. Then nuclei of somatic destination eliminate the "limited" chromosomes, and shortly thereafter one or both paternal X chromosomes (one in female-production, both in male-production). Thus the "limited" chromosomes are restricted to the germ-line and are not found in somatic tissues. This fact is responsible for our failure to detect these chromosomes in females during the early stages of our work. There is also an elimination of one paternal X (and presumably sometimes a superfluous "limited" chromosome) from the germ-line (see below), but in both sexes two X chromosomes remain in the germ-line.

(4) *Gametogenesis.* Oogenesis follows the usual pattern, with random segregation of chromosomes (genetic and cytological evidence). Spermatogenesis is highly aberrant. There is apparently no synapsis here (cytologi-

cal evidence); a monocentric mitotic figure appears at the
first spermatocyte division; maternal chromosomes all go
to the single pole and into the second spermatocyte (see
5, below); paternal chromosomes all go away from the
pole and are discarded, except "limited" chromosomes,
all of which go to the pole. The second spermatocytes
are all alike; each contains only maternal chromosomes
except as regards the "limited" chromosomes. The sec-
ond division is also asymmetrical; all chromosomes except
the X divide and send daughter halves to opposite poles;
the X divides, but both sister halves go to one pole; this
pole is retained in the spermatid; the other is pinched off
in a bud and degenerates. Hence instead of four sperms
from each primary spermatocyte there is only one; and
instead of two classes of sperms (X-bearing and no X- or
Y-bearing) there is only one and it transmits two sister
maternal X's.

(5) *Inheritance.* The distribution of maternal and
paternal chromosomes just described is based on genetic
as well as cytological evidence. Inheritance through the
female is of the ordinary Mendelian type, with random
segregation and crossing over. The male, however, trans-
mits only maternal genes, although he manifests genetic
characters due to genes received from his father.

(6) *Sex ratios and sex chromosome behavior.* Instead
of giving males and females in equal numbers a pair mat-
ing in *Sciara coprophila* gives practically all males or
practically all females. (In some of the other species the
process is modified but still not "typical"—see p. 493).
The sex of the family depends on the mother. Instead of
all females being alike as regards sex chromosome con-
stitution there are two kinds, produced in equal numbers.
Male-producers are XX; female-producers XX', the X'
chromosome differing genetically from the X (see p. 492).
Presumably this mechanism, through influence on the cyto-
plasm of the eggs, essentially controls the type of chro-
mosome elimination which will occur in the eggs produced
by a given female, and hence indirectly exerts a more or

less definite predetermining influence on sex (p. 509).   The presence of "exceptional" males in female families, and *vice versa,* however, shows that each type of female is potentially capable of producing both sons and daughters.

(7) *Sex determination.*   In Sciara the sex of the individual fly, instead of being determined at fertilization by the type of sperm fertilizing the egg, is determined during embryonic development by the type of chromosome elimination occurring during cleavage.   Where two X chromosomes, or X and X′, are retained in the soma a female results, and where only one X is retained a male results (even though the germ-line is XX) as described more fully below.   Thus males and ♂-producing females arise from fertilized eggs which started out with the same chromosome constitution.   On this basis the only simple interpretation is that sex is determined by the chromosome constitution of the soma, irrespective of that of the gonads themselves.   No explanation is yet apparent for some of the main peculiarities of sex chromosome behavior, but some suggestions as to their possible significance will be presented below (p. 512).

(8) *Features of special cytological interest.*   The monocentric first spermatocyte mitosis, with accurate segregation of chromosomes in a unipolar field, possesses special interest in connection with problems of chromosome behavior and the mechanism of mitosis and meiosis. Equal interest attaches to the precocious movement of both halves of the X chromosome to one predetermined pole at the second spermatocyte division and to the selective elimination of chromosomes during cleavage.   Chromosomes presumably identical in genic constitution are differentiated, and their behavior determined, by influences due to the sex of the parent from which they are derived. These features will be discussed under the appropriate headings below.

Sex Ratios

Since nearly all the phenomena under consideration bear directly or indirectly on problems of sex the topic of sex ratios will be treated first.

Unisexual families. On the basis of sex ratios two types of reproduction are found in Sciara, as indicated in earlier papers (Metz, 1925a, 1926a; Metz, Moses and Hoppe, 1926; Metz, 1927; Moses and Metz, 1928; Metz and Moses, 1928; Metz, 1929b, c,; Metz and Schmuck, 1929a, b; etc.). Some species exhibit one, some the other and some both, as will be explained later. One is characterized by the production of "unisexual" families. Here the offspring from any pair mating are all or nearly all of one sex, either male or female. The sex of the entire family or the "progeny as a whole" is determined by the female parent.. There are two types of females; one ♂-producing, the other ♀-producing. As shown by genetic evidence in the papers just cited, these are produced in equal numbers in the female progenies and differ in respect to one sex chromosome, as indicated schematically in Fig. 2. Both types of females possess two X chromo-
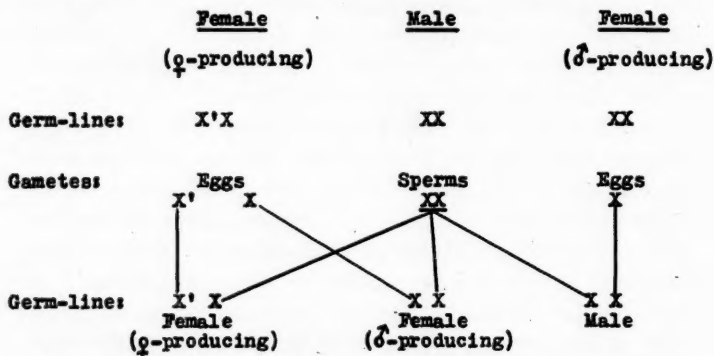

Fig. 2. Diagram illustrating the sex chromosome mechanism responsible for production of "unisexual" families in *Sciara coprophila.* See text for explanation.

somes. In male-producers the two are alike (XX); but in female-producers one differs genetically and is designated X-prime (X'), giving the constitution X'X.

As will be shown below, the males all appear to have the same chromosome constitution and to produce only *one type of sperm,* so they may be left out of account so far

as sex ratios are concerned. Experiments have shown
(Metz and Moses, 1928, Moses and Metz, 1928, etc.) that
the male apparently has no influence on the sex ratio in
his offspring.

Since ♂-producing and ♀-producing females appear in
a 1:1 ratio the total number of males and of females in
the population is kept approximately equal. Apparently
the main general effect of such a mode of reproduction
would be to minimize inbreeding and insure a relatively
large amount of outcrossing in the population as a whole.

In these "unisexual" families "exceptional" indi-
viduals appear which are not of the expected sex. These
are particularly interesting for several reasons and will
receive special consideration in a later section (p. 512).
As noted above their presence shows that all the females
are potentially capable of producing offspring of both
sexes and that the mechanism or agency responsible for
the sex of the progeny as a whole is not the final sex-
determining agency itself.

Bisexual families. In contrast to the type of reproduc-
tion just described there is another in which the families
consistently include both sexes. At first sight this seems
to resemble the ordinary type found in "typical" animals;
but actually it appears to be fundamentally different and
to be essentially a modification of the type involving uni-
sexual families. Instead of sex ratios of the ordinary
1:1 type, or of the unisexual type just mentioned, the
ratios here vary through a wide range. The reasons for
this are not yet understood, and since this mode of repro-
duction has not yet been investigated adequately it will
receive only brief consideration. The main point of pres-
ent interest is the relationship between the two modes of
reproduction. It might be argued that they are not
actually different and that a continuous range of condi-
tions exists from that which gives ratios of 1:0 or 0:1
to the opposite which gives 1:1. In one sense this may be
true, for ratios from one extreme to the other may be
found; but that there is a real distinction in nature is

shown by the fact that certain species consistently exhibit one type of behavior and others the other.

Sex ratios in different species. Fourteen species of Sciara have been studied by the writer sufficiently to ascertain the types of sex ratios produced, and six of these have been studied extensively enough to indicate whether or not their behavior is consistent. The results seem to show clearly that certain species are characteristically of one type and others characteristically of the other, while others include strains of both types. For example, *S. coprophila* Lint. and *S. impatiens* Joh., both widely distributed throughout the United States, have thus far been found consistently to give only "unisexual" families, except for a mutant laboratory strain of the former (Metz and Moses, 1928; J. P. Reynolds, in press) and an apparently similar strain from one female of the latter.

Similarly, *S. pauciseta* Felt and *S. prolifica* Felt, equally widely distributed, have uniformly given bisexual families. The sex ratios, although variable, are consistently different from those produced by the other species mentioned. Three other species, all apparently undescribed, have been found to give sex ratios of this type, but these species have not been studied extensively. Among the other species which have not been studied extensively are five which appear to be of the "unisexual family" type, including *S. varians* Joh., *S. subtrivialis* Petty and three unidentified species.

In contrast to the species consistently exhibiting only one type of reproduction are two which exhibit both: *S. similans* Joh. and *S. ocellaris* Comst. The latter has been studied extensively. Strains of both types may be secured in nature in the same locality, and are interfertile when crossed. The genetic basis of the distinction between them is under investigation and will be treated elsewhere; but the results already obtained seem to make it clear, as intimated above, that the distinction between the two types of reproduction is not fundamental. It probably represents a difference of one or a few genes. There

are some data (E. Gay Lawrence and Helen V. Crouse, unpublished) which suggest that the variable sex ratios in the bisexual families may be due to crossing over between two kinds of X chromosomes here, but the evidence is not yet complete.

DIFFERENT TYPES OF CHROMOSOMES IN SCIARA

Another topic which may be considered independently is the present, dealing with the distinction between the "ordinary" chromosomes and those which are referred to as the "limited" chromosomes because they are found only in the germ-line, not the soma. In our earlier papers, up to 1931, the "limited" chromosomes were described as present in the male only, and were referred to as "male-limited" or "androsomes" because the chromosome group of the ovarian follicle cells was considered to represent the definitive group for the individual, as in other organisms. Later it was found that the "limited" chromosomes are present in both sexes, but only in the germ-line (Metz and Schmuck, 1931 a, b, Metz, 1931 a). These chromosomes are readily identified both by appearance and by behavior, and are found in all but two (*S. ocellaris* Comst. and *S. reynoldsi* Metz) of the species thus far studied, including most of those listed above. Their main characteristics appear to be the same in all species possessing them, so conditions in the best known species, *S. coprophila,* may be used for illustration. These are summarized below.

(1) The limited chromosomes are larger than the others and often show the unusual characteristic of having a greater diameter as well as length (Fig. 3, see also photographs: Metz, Moses and Hoppe, 1926 Fig. H, p. 250; Metz, 1936, Fig. 2, p. 223). This greater thickness is interesting because it probably reflects a somewhat different internal organization. Their foundation structure is apparently a coiled chromonema, as in other chromosomes (unpublished evidence of A. L. TerLouw and the writer), but it seems necessary to assume that this has a wider coil than the others to account for the chromosome

diameter. Although apparently "empty" or "inert" for the most part, as regards genes, these chromosomes reproduce and go through the essential mitotic and interphase transformations along with the other chromosomes. If the chromonema is really mainly non-genic it is evident that the non-genic basis has continuity and power of reproduction, unless we assume that it is fabricated anew in each cell generation (see Muller and Gershenson, 1935). Unfortunately, it has been impossible thus far to examine the structure of these chromosomes by the method used for the others because they are eliminated from the somatic cells and hence are not represented among the giant chromosomes in the salivary glands.

(2) In the present species each individual fly presumably requires one complete limited chromosome, or its

Fig. 3. Polar view of second spermatocyte metaphase in *Sciara pauciseta* Felt; traced from photograph shown in an earlier paper (Metz, 1936, Fig. 2). The X chromosome has already gone to one pole (see Fig. 6) and is not shown here. Note the great thickness as well as length of the two "limited" chromosomes (L).

equivalent, for normal development; but addition of one or two more apparently has no serious effect. Three is the largest number observed in any one individual.

(3) Not only do the limited chromosomes vary in number, as just indicated, but they apparently fragment readily, and numerous fragments may be present in the germ-line without obvious effect on the fly.

(4) In the first spermatocyte the limited chromosomes remain condensed or "heteropycnotic" in the manner characteristic of sex chromosomes in many other organisms. This suggests that they may once have been true sex chromosomes; but there is no evidence that they have any sex-determining function at present. Indeed, it seems clear that they do not have such function, both be-

cause of their behavior and because two species, which otherwise show the same chromosomal and genetic characteristics as the others, do not possess them. One of these species is *S. ocellaris,* on which much genetic and cytological work has been done.

From the evidence just summarized several conclusions are drawn as to the nature of the limited chromosomes. One is that there is fundamentally just one kind of limited chromosome, not two as was thought at first (Metz, 1925 a) when two dissimilar ones were found in *S. similans* Joh. The smaller one in that case was presumably derived by loss of a fragment. Another is that the limited chromosome is a true chromosome, not merely a chromatoid body. It presumably contains one or a few, but not many, vital genes. A third is that from the evolutionary standpoint these chromosomes are probably in process of disappearing. And a fourth is that their vital function is important only for gonad development, or early cleavage stages, because these chromosomes are eliminated from the somatic nuclei at an early cleavage stage.

Oogenesis in Sciara

In most animals gametogenesis conforms to an essentially similar pattern in both sexes so far as chromosome behavior is concerned, but in Sciara the process of spermatogenesis is widely different from that of oogenesis in this respect. Oogenesis appears to conform to the standard type as indicated by both genetic (Metz, 1926 c, 1927, etc.) and cytological (Schmuck and Metz, 1932) evidence. The chromosomes undergo synapsis, exhibit random segregation and regular distribution; genetic crossing over occurs and the meiotic divisions involve no cytological peculiarities, so far as known. The primary oocyte contains four pairs of "ordinary" chromosomes in all species thus far studied, and the egg nucleus receives one member of each. In *S. coprophila* and presumably in other species possessing "limited" chromosomes, the oocyte also contains one or more chromosomes of this

type. (Schmuck and Metz, 1932, and unpublished evidence). If two "limited" chromosomes are present they apparently undergo synapsis and segregation in the usual manner. If only one is present it apparently segregates at random, although the evidence is not conclusive on this point. In any event it seems clear that many eggs transmit one or more "limited" chromosomes in addition to the four "ordinary" ones.

Spermatogenesis, in contrast, exhibits so many peculiarities that it requires separate treatment.

SPERMATOGENESIS

Some of the most aberrant phenomena exhibited by Sciara occur during spermatogenesis, and since these hold the key to an understanding of most of the others they will be considered in some detail. They have been described in earlier papers (Metz, 1925 a; Metz, Moses and Hoppe, 1926; Metz, 1933). In essentials spermatogenesis follows the same pattern in all the species studied, including most of those listed above. The important points for present consideration are the following, which are taken from the best known species, *S. coprophila*.

CONDITIONS IN SPERMATOGONIA

(1) In the later generations of spermatogonia, shortly before onset of meiosis, there are two each of the "ordinary" chromosomes present (Fig. 4, 1) but they are not associated in pairs in the manner characteristic of most Diptera. This latter fact is interesting because in the somatic nuclei here there is conspicuous, intimate prophase pairing of homologues just as in other Diptera.

(2) Four pairs of "ordinary" chromosomes are found at this stage in this and all the other species examined. In this species they consist of one V-shaped pair and three rod-like pairs (Fig. 4, 1). In some other species *(e.g. S. similans, S. prolifica, S. pauciseta)* two pairs of V's and two of rods are present (Metz, 1926 a; Metz, Moses and Hoppe, 1926; Schmuck, 1934).

(3) In *S. coprophila* one of the three rod-like pairs is

the sex chromosome pair.   In *S. pauciseta,* which has the other type of group (two rod-like and two V-shaped pairs), the sex chromosomes are V-shaped (Schmuck, 1934).

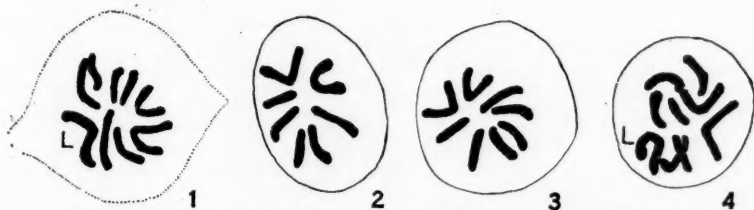(4) One or more "limited" chromosomes are present (L, in Fig. 4).

Fɪɢ. 4. Chromosomes in *Sciara coprophila* Lintner. 1, spermatogonial group; 2, somatic group of male; 3, somatic group of female; 4, oogonial group. (L), the "limited" chromosome. In comparing these groups it should be borne in mind that, whereas homologous chromosomes associate in pairs in somatic cells, they apparently do not do this in oogonia or spermatogonia. It should also be noted that in 1 and 4 the chromosomes do not all lie in a horizontal plane; hence there is some distortion due to foreshortening. (From Metz and Schmuck, 1931).

Conditions in the First Spermatocyte[2]

(1) The first peculiarity to be observed during the growth period of the primary spermatocyte is the absence of synapsis. The individual chromosomes apparently remain separate from one another just as they do in the spermatogonia, although in other respects the growth period is not conspicuously different from that in other Diptera.

(2) As noted above, the "limited" chromosomes remain condensed during this period and in this respect resemble the sex chromosomes of other diptera.   Presumably the true sex chromosomes do not remain condensed, although the evidence on this point is not yet satisfactory.

(3) The most extraordinary characteristic of the first spermatocyte is the monocentric or unipolar mitosis which it exhibits, and the accurate process of segregation of chromosomes effected by this unipolar mechanism. Its

[2] See Metz, Moses and Hoppe, 1926; Metz, 1933.

cytological aspects will be considered separately in a later section (p. 515).

(4) At this monocentric mitosis the maternal "ordinary" chromosomes, and all the "limited" chromosomes, regardless of number, pass to the single pole (Fig. 5).
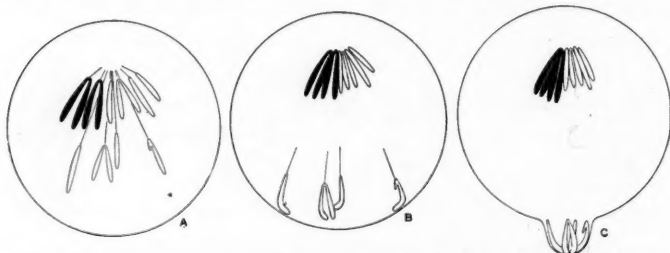

Fig. 5. Diagrams representing three stages in the unipolar first spermatocyte division (*Sciara coprophila*). See text for explanation. The four chromosomes which retreat from the pole and are pinched off are the paternal X and autosomes; note their reverse orientation. The "limited" chromosomes are shown in solid black.

As shown by genetic evidence there is completely selective segregation of homologues among the ordinary chromosomes such that the maternal member of each pair goes toward the pole, and the paternal member goes away from it (Metz, 1926 c, 1927, 1928, etc.; Smith-Stocking, 1936). This is effected in spite of the fact that the chromosomes do not unite in pairs and do not become oriented on an equatorial plate before they segregate.

(5) The first spermatocyte mitosis is asymmetrical and resembles in some respects polar body formation in an egg. The paternal chromosomes which pass away from the pole are extruded in a small polar-body-like process (Fig. 5) which is pinched off and later degenerates.

(6) As a result the paternal chromosomes are entirely lost and only the maternal derivatives are passed on to the second spermatocytes—except as regards the "limited" chromosomes, which are all retained.

The Second Spermatocyte Division

(1) The second spermatocyte division, following closely after the first, exhibits further peculiarities. It is bi-

polar; but one pole of the mitotic figure appears in advance of the other. All the chromosomes divide at this mitosis, and the daughter halves of all but one go to opposite poles. One chromosome passes bodily to the first pole formed, in advance of the others and before its two halves separate from one another, as shown in Fig. 6.
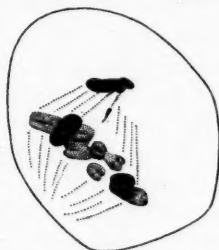

FIG. 6. Side view of second spermatocyte metaphase in *Sciara coprophila*, showing the precocious movement of the split X chromosome to one pole and the distortion produced in one chromatid by the ''pull'' of the spindle fiber extending toward the opposite pole. From a camera drawing.

This chromosome is called the ''precocious'' chromosome because of this precocious movement. It is almost certainly the sex chromosome, and since it is maternal in origin it should be an X chromosome.

(2) Like the first division, this one is asymmetrical and gives rise to a large cell and to a small rudimentary process which subsequently degenerates. The complete cell, forming a functional spermatid, contains the pole of the spindle which formed in advance of the other and which received the divided ''precocious'' chromosome.

The net result of spermatogenesis, so far as chromosome distribution is concerned, is that all the sperms are alike, each contains the complete set of maternal chromosomes, plus a duplicate of the X, and no paternal chromosomes at all, except presumably in the case of the limited chromosomes.

PROBLEMS PRESENTED BY PECULIARITIES OF
SPERMATOGENESIS

Each of the phenomena under consideration presents its own problems, and it will facilitate subsequent discussion

to consider these somewhat before passing on to other
features. Leaving out of account those bearing on the
mechanism of mitosis, which will be treated separately
below, the most important ones seem to be associated with:
(a) the absence of pairing of chromosomes in spermato-
gonia and of synapsis in the primary spermatocytes; (b)
the absence of the usual random segregation of chromo-
somes in meiosis, and the presence, instead, of a highly
selective segregation in which, *without previous synapsis,*
paternal chromosomes are separated as a group from the
maternal homologues; (c) the occurrence of two asym-
metrical divisions, and consequent elimination of one
chromosome group at each—including the complete elim-
ination of the paternal "ordinary" chromosomes; (d) the
regular transmission of two duplicate (sister) sex chro-
mosomes by each sperm, and (e) the fact that only one
sperm is derived from an original spermatocyte and that
all sperms are alike in chromosome constitution.

There is no obvious explanation for the failure of the
chromosomes to unite in synapsis here. Lack of synapsis
is not due to dissimilarity or incompatibility of the chro-
mosomes themselves, because in the somatic nuclei in-
timate synapsis of homologues occurs, as shown especially
clearly in the giant salivary gland nuclei. There is no
evidence that the phenomena can be explained on the
basis of the general hypothesis of Darlington that in all
organisms chromosomes pair when single (containing only
one chromonema each) and not when double. Any such
view is opposed by the intimate association of homologous
chromosomes in triploids and by the evidence from
multiple chromosome complexes, especially that presented
by Berger (1936, 1937), showing that even when each
chromosome is multiplied several times homologues and
sisters all become associated. It seems probable that
lack of synapsis is due to some materials or activities of
the cells and not to any condition of the chromosomes
themselves. Presumably absence of synapsis is to be
interpreted in connection with the selective segregation of

maternal from paternal chromosomes. If synapsis *and* crossing over occurred, maternal and paternal chromosomes would not remain intact, hence selective segregation might be interfered with, especially if, as seems probable (see second paragraph below), it depends on characteristics of the entire chromosomes rather than restricted loci. But absence of crossing over alone would presumably have the same effect. It may also be suggested that the monocentric mitotic mechanism might not function if homologues were in intimate contact, but that again is questionable.

One of the most interesting phenomena in Sciara is the monocentric first spermatocyte division with its highly selective segregation of chromosomes. The monocentric mitotic figure is highly aberrant, but there is no obvious reason why it should result in selective segregation; and since the chromosomes are all apparently separate from one another and free to move in any direction and are apparently all in the same condition, ready for mitotic movement, there is nothing about them which would seem to influence the process.

The most reasonable interpretation of the process seems to be that previously suggested (Metz, 1925 b, 1933, 1936; Metz, Moses and Hoppe, 1926) *i.e.*, that the difference in behavior is due to a general qualitative difference between maternal and paternal chromosomes (except the "limited" chromosomes), and that this is impressed on the chromosomes in the preceding generation by the sex of the parent. On this interpretation homologous chromosomes, which possess the same sets of genes, react in opposite ways at the reduction division because of this qualitative difference. It should be emphasized that this qualitative difference or modification persists for only one generation and is reversible. The same chromosomes which are maternal in origin and hence pass to the pole in the males of one generation become paternal chromosomes which pass away from the pole in the males of the next generation. This fact has been demonstrated by

abundant genetic evidence from four species of Sciara (*e.g.,* Metz, 1926 a, 1927, 1928, 1929 a; Smith-Stocking, 1936; and unpublished evidence). The reason for considering the qualitative difference between maternal and paternal chromosomes to be distributed through the chromosome rather than localized, is that the movement of the paternal chromosomes away from the pole appears to be due to such a widely distributed quality and not to any characteristic of the "spindle fiber locus"—as noted in the papers cited at the beginning of this paragraph.

Why the two spermatocyte divisions should be asymmetrical and why the paternal chromosomes should be discarded, instead of being transmitted as they are in other organisms, is unknown. The elimination can not be due to any fundamental genic peculiarity of the chromosomes, because it is clear from genetic evidence that these chromosomes do not differ in this respect from their homologues, and also because, as just noted, those which react in one way and are retained in one generation may be eliminated in the next. At first it seemed possible that special significance should be attached to the behavior of the "limited" chromosomes, and the fact that they are regularly retained along with the maternal ordinary chromosomes, but at best this could only help to explain the asymmetry of the division, not the selective segregation, and even this possibility is weakened by the fact that in the species which lack the "limited" chromosomes the same peculiarities of mitosis and segregation are present.

From the standpoint of sex determination the greatest puzzle presented by spermatogenesis comes from the fact that only the maternal sex chromosome (X) is transmitted to the second spermatocyte, and that both daughter halves of this chromosome then pass together into the final spermatid at the second spermatocyte division. There seems to be no question about the facts here either as regards the genetic or cytological evidence. Apparently the only possible loophole would be a mistake in identifying the "precocious" chromosome of the second

spermatocyte with the sex chromosome.   The evidence
all points to the correctness of this identification, how-
ever, and there seems to be no plausible alternative.

The possible significance of these processes will be con-
sidered later, after the further history of the sex chromo-
some is reviewed (p. 511).

Chromosome Elimination During Cleavage

This aspect of the subject has been investigated espe-
cially by Dr. Anne M. DuBois (DuBois, 1932, 1933), using
mainly *S. coprophila,* to which the present summary ap-
plies.   The observations were supplemented by study of
S. ocellaris, showing that sex chromosome elimination
follows the same pattern in a species having no "limited"
chromosomes.

Since the fertilized egg contains ten or more chromo-
somes (four or five from the egg nucleus and six or more
from the sperm), but the somatic cells of the embryo de-
veloping from it contain only seven, in the male, and eight
in the female (Metz, 1931 a) it is evident that a reduction
in number has occurred during the intervening stages.
The nature of the processes responsible for this reduction
is indicated below, and the results are illustrated sche-
matically in Fig. 1.   From these it will be seen that a
precise mechanism is involved, that the process is not
confined to the "limited" chromosomes, but involves sex
chromosomes as well, and that the elimination differs in
the two sexes and probably plays a part in sex determi-
nation.

In the case of the germ-line, as distinguished from the
soma, it seems clear that a comparable process of chro-
mosome elimination occurs; but it has not yet been ob-
served directly.   It will be considered briefly after
somatic elimination is reviewed.

During the first four cleavage divisions of the fertilized
egg the nuclei migrate from the center toward the periph-
ery of the egg, and those which will ultimately give rise
to the germ cells become set apart at one end of the egg,
where they and their descendants are readily distin-

guished thenceforth.   Thus germ-line and soma are defi-
nitely separated at an early stage, as in other Diptera.
At the fifth or sixth cleavage division the nuclei of the
somatic line lose the "limited" chromosomes (Fig. 7).
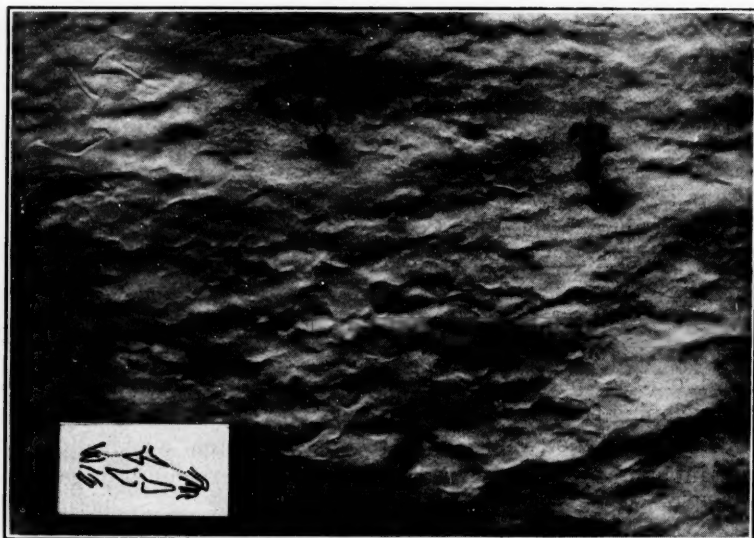

FIG. 7.   Photograph of a portion of an entire egg of *Sciara coprophila*,
at one focal level.   Sixth cleavage division showing simultaneous elimination
of the two large "limited" chromosomes at anaphase in all mitoses of por-
tion destined to produce somatic tissue.   These chromosomes are seen in each
case lagging near the equator between the two groups which have gone to
the poles.   Note that the "limited" chromosomes divide, and the daughter
halves may separate, as shown at the lower left, but they do not reach the
poles.   The insert is a diagram interpreting the figure just above it.   Some
of the chromosomes at the poles are out of focus and are not shown.

These chromosomes lag during mitosis, remaining near
the equator of the spindle into telophase when the
daughter nuclei are formed at the two poles.   Thus they
are left free in the cytoplasm, where they ultimately de-
generate.   For one or two cell generations after elimina-
tion they apparently go through the usual cycle of
changes, including division, outside the nuclei, but their
activity gradually becomes delayed as compared with that

of those in the nuclei (Metz, unpublished). So far as known this first elimination process occurs in all species possessing "limited" chromosomes.

The "limited" chromosomes are all eliminated at once, regardless of whether the number is one, two or more; and the process occurs essentially simultaneously in all somatic nuclei, because mitoses are synchronous during cleavage. No elimination occurs in the germ-line nuclei at this time, so far as known.

At the seventh or eighth cleavage division a second and similar elimination process occurs. This involves the sex chromosomes and differs in the two sexes (Fig. 1). In eggs destined to produce females a single rod-like chromosome is eliminated (in *S. coprophila*). Since four symmetrical pairs of chromosomes remain in the soma after this elimination (Metz, 1925a, 1926a, etc.) and since genetic evidence shows that each pair includes a maternal and paternal member (Metz, 1926 c, 1927, etc.; Smith-Stocking, 1936) it seems clear that the eliminated chromosome is one of the two sister chromosomes transmitted by the sperm, as described above (Fig. 1). It will be recalled that these sisters are derived from the "precocious" chromosome of the second spermatocyte and are X chromosomes (see below).

In eggs destined to produce males a comparable second elimination occurs, but it involves two chromosomes. One of these is evidently similar to that eliminated in female-producing eggs—*i.e.*, derived from the "precocious" chromosome of the father. The other is presumably its sister. In other words, both products of the "precocious" chromosome appear to be eliminated here. This conclusion is based mainly on three lines of evidence: (1) the morphological similarity of the two chromosomes, (2) the fact that this similarity holds also in species in which the "precocious" chromosome is V-shaped instead of rod-like (Schmuck, 1934) and (3) the evidence which indicates that the chromosomes in question are sex chromosomes and are paternal in origin. This latter point will be considered below under sex determination.

CHROMOSOME ELIMINATION IN THE GERM-LINE

Chromosome elimination in the germ-line, although not yet directly observed, presumably occurs in a manner comparable to that in the soma, and probably at a somewhat later stage—perhaps correlated with the germ-cell migration from the pole of the egg to the interior prior to gonad formation. Careful study has revealed no evidence of elimination prior to this migration (Metz, unpublished), yet spermatogonia and oogonia at an early larval stage have apparently already lost one or more chromosomes. The time of elimination is important because of its possible bearing on sex determination, but unfortunately it can at present only be located within the limits just indicated.[3]

It seems clear, from the cytological and genetic evidence already cited, that an elimination of one "ordinary" chromosome occurs regularly in the germ-line nuclei of all eggs and that it is one of the two sister derivatives of the "precocious" chromosome from the father. In the case of the female the evidence appears to be complete in this respect, for oogonial figures show the expected eight "ordinary" chromosomes, all of which have been identified and traced into the descendants by genetic means (Metz, 1926 c, 1928, 1929 a, Smith-Stocking, 1936). In the male this latter test is impossible, because of the failure of the male to transmit any paternal chromosomes (owing to the aberrant type of spermatocyte divisions), but nevertheless the evidence seems conclusive.

Presumably an elimination of one or more "limited" chromosomes may also occur in the germ-line in some cases. Such an inference seems to be required by the fact that the number of "limited" chromosomes does not become excessive as would be expected if there were no regulatory process to prevent it. It will be recalled that there is no segregation of "limited" chromosomes in

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[3] Since this paper went to press Mr. R. O. Berry has secured evidence (unpublished) which seems to indicate that elimination from the germ-line occurs after the germ cells have migrated to the definitive position of the future gonads.

spermatogenesis and that each sperm receives and presumably transmits the full number present in the spermatocyte—at least one and often two or three. Since the egg may also transmit one (possibly more) a mechanism is provided for gradually increasing the number of such chromosomes unless a regulatory process intervenes. Observations on the transmission of fragments of the "limited" chromosome (A. L. TerLouw, unpublished) make it probable that ordinarily those of maternal origin are not eliminated, but those of paternal origin are eliminated from the germ-line during development. Presumably this principle applies to entire "limited" chromosomes also and is effective in keeping their number within the limits indicated.

SEX DETERMINATION

It will be observed that the sex chromosome mechanism outlined above results in a type of sex-linked inheritance like that shown by ordinary organisms in which females are X X and males XY and sex is determined by the type of sperm fertilizing the egg. This led for a time to the assumption that an ordinary XY mechanism is present in Sciara and that the production of unisexual families is due to selective fertilization or selective elimination of gametes (Metz, 1929 b). Present evidence, however, as already intimated, points directly to the interpretation that sex is determined here by the chromosome constitution of the soma, which is in turn due to the process of chromosome elimination during cleavage (Metz, 1931 a, b). It seems highly probable that this interpretation is correct; but in view of the fact that apparently well-founded previous interpretations in Sciara have proved to be wrong and that several aspects of sex chromosome behavior here are not yet explained, it is desirable to consider all possibilities, however remote, and to lay especial emphasis on any uncertain points. The present discussion is designed for this purpose.

Two types of interpretation have previously been proposed which differ mainly in the significance attributed

to the unisexual families. DuBois (1933) has suggested that sex may essentially be determined by the cytoplasmic constitution of the egg before fertilization, due to the sex chromosome constitution of the mother. On this view the unfertilized eggs of XX' mothers possess a female quality or tendency and those of XX mothers a male quality or tendency. The interpretation was supported by the fact that in gynandromorphs of *S. coprophila* the two gonads were consistently alike. To the extent that it assumes a predisposition in the unfertilized egg this interpretation is apparently correct, but it is difficult to consider the initial tendency a true sex characteristic because, as she points out, what it apparently does is to influence the process of chromosome elimination, and also because of the fact that some eggs from XX' mothers may develop into males and some from XX mothers into females. As noted above this latter fact seems to show that in each case the eggs have the potentiality of developing into either sex, and that the end result is determined by the type of chromosome elimination which occurs in the embryo. Furthermore, recent unpublished evidence of Mrs. E. G. Lawrence and Miss H. V. Crouse shows that frequently in *S. ocellaris* individual gynandromorphs possess both an ovary and a testis, showing that the nature of the gonads here is not predetermined by the general constitution of the unfertilized egg.

The other type of view (Metz, 1930, 1931 a, b) is that outlined in the present paper, which considers sex as not established until after chromosome elimination has occurred during development. In considering the nature and significance of chromosome elimination interest centers on the distinction between conditions in the soma and those in the germ-line. The large "limited" chromosomes may be ignored in this connection, for they apparently have no direct influence on sex determination and, as already noted, are absent from some species. Likewise, the distribution of the autosomes may apparently be ignored, for they are not affected by the elimination

process. This leaves only the sex chromosomes. No distinction need be made at the moment between reproduction which gives "unisexual" and that which gives bisexual families, because elimination appears to be the same in both. As indicated in Fig. 1 each fertilized egg receives one X from the mother and two (sisters) from the father—the latter two derived from the maternal X in the father. As the egg develops, the nuclei of the somatic line lose both of the X chromosomes from the father, in case it develops into a male, or one of them if it develops into a female. Thus the male soma comes to be XO and the female soma XX. This suffices as an explanation of sex determination, at least so far as the nature of the soma is concerned, and it is supported by evidence from gynandromorphs in which the distribution of sex-linked genes shows that the male tissue possesses one X and the female tissue two.

Conditions in the germ-line, *i.e.*, the gonads themselves, have already been described (Figs. 1 and 4). Spermatogonial and spermatocyte, as well as oogonial and oocyte figures, show two sex chromosomes retained in the germ-line after chromosome elimination has taken place. Since these should both be X chromosomes in each case, as indicated by their derivation, it would appear that ovary and testis develop with the same chromosome group and that the nature of the gonads is determined by that of the soma.

The only difficulties with this type of interpretation are that it involves the assumption of non-independent development of the gonads, which is not definitely known to apply generally to insects, and that it gives no explanation for some of the most remarkable peculiarities in sex chromosome behavior in, Sciara. It leaves unexplained the "precocious" behavior of the X chromosome, the transmission of two sister X chromosomes by each sperm and the regular elimination of one of these from all cells, somatic and germinal. Much effort has been devoted toward getting some clue as to the meaning of these latter

phenomena which, because of their peculiar nature, their constancy and their wide-spread distribution, must be considered to have special significance. Two facts are particularly perplexing: One is that although apparently two X chromosomes are regularly transmitted by all sperms, they are not both retained in any tissue of the organism so far as known (and the evidence seems conclusive). The other is that, although these two chromosomes are sisters and presumably identical, one is regularly eliminated without the other (in all cells during development of a female and in cells of the germ-line in development of a male). It is exceedingly difficult to conceive of a mechanism in the cell which could regularly effect such a process. The writer has studied intensively the elimination figures, using entire, unsectioned eggs (for method see Schmuck and Metz, 1931) without finding any indication that the elimination can be explained on a mechanical basis, such as crowding, position on the spindle, etc. The difficulty thus presented has even led to the suggestion (Metz, 1930) that the two sister chromosomes under consideration are not alike at the time of elimination and that the difference between them may have special significance in connection with sex determination. It was suggested that the peculiar precocious movement to the pole in the second spermatocyte served to alter or inactivate part of one, through action of the "spindle fiber" extending toward the opposite pole (see also Metz, 1936) and that this chromosome may, therefore, function as ·a "Y" rather than an X; also that the "Y" is retained and the X eliminated in the production of a testis, and the reverse in the case of the ovary. Such an interpretation seems improbable, but it is the only one thus far advanced which attempts to interpret the entire series of phenomena.

Significance of "Exceptional" Flies and of Bisexual Families

Among the phenomena which are not yet understood are those responsible for the production of bisexual families and those responsible for the appearance of "excep-

tional" individuals in "unisexual" families. Pending
further analysis only a few comments need be made on
these in addition to what has been given in preceding
paragraphs. There is evidence that a few exceptional
flies result from non-disjunction or other abnormal phe-
nomena, but most of them do not. Most exceptional males
receive the X, rather than the X', chromosome from the
mother and are indistinguishable in genetic behavior from
ordinary males from male progenies. A few, however,
receive the X' chromosome. These are indistinguishable
in external appearance from ordinary males, showing
that the X' chromosome is not radically different from the
X. Most of them are sterile, but some are fertile and ex-
hibit the expected genetic behavior (Metz and Schmuck,
1929b). "Exceptional" females, as would be expected,
are XX and indistinguishable in appearance and behavior
from ordinary male-producing females (Metz and Moses,
1928). It seems evident from these facts that most "ex-
ceptional" flies, of either sex, are ordinary males or
females which have developed in the manner character-
istic of their sex—*i.e.*, chromosome elimination has oc-
curred in the normal manner, but has been of the opposite
type from that expected. Apparently in these particular
eggs something has counteracted the influence or changed
the balance set up by the zygotic chromosome group of
the mother so that an egg from an X'X mother develops
in the manner expected of one from an XX mother, and
vice versa. It seems simplest, for the time being, to ex-
plain this on a quantitative basis, assuming a balance
between genes in the different chromosomes and a thresh-
old value separating the two types. Presumably chromo-
some elimination, like other characters, depends upon the
interaction of numerous genes in both autosomes and sex
chromosomes, and the X' possesses one or more which are
ordinarily dominant. Different combinations of auto-
somes or of genes in the sex chromosomes or allelomorphs
of different "strength" may throw the balance so close to
the threshold value that in some eggs the threshold is

passed and chromosome elimination follows the opposite pattern from that expected. It is also possible that, although chromosome elimination is usually predetermined before maturation of the egg, it may be influenced to some extent by the chromosome constitution of the egg after maturation (which follows fertilization) and that this may play a part in causing the production of "exceptional" individuals. For example, if X' and X exert opposing influences, an egg from an X'X mother may not have the influence of X' firmly established before maturation, so the X remaining after maturation may exert enough influence to bring about the male-producing type of elimination. This might account for the scarcity of X' males among the "exceptionals," although it is difficult to explain the production of any such males on this basis. Likewise it is difficult on this basis to explain the production of "exceptional" females, except by assuming different strengths of X and the possible influence of the paternal X after fertilization.

The problem presented by bisexual families is presumably closely related to that just discussed and may be essentially the same, for, superficially at least, a bisexual family here is simply one with a larger number of exceptional individuals. The fact that some species regularly give "unisexual" families, others regularly give bisexual families, and still others possess interfertile strains of both types, indicates that we are dealing with a range or series of modifications of one fundamental chromosome mechanism.

It seems significant that in species regularly giving bisexual progenies, such as *S. pauciseta,* the sex ratio varies through a wide range on both sides of 1:1. This suggests that a modified X'X mechanism is present, but with less distinction between X' and X. The fact that no females appear to be simple XX male-producers suggests that all females are heterozygous as regards their sex chromosomes. Hence they have been provisionally designated X"X, using X" to represent a modified counter-

part of X'. On this basis, however, it would be expected
that all females would be alike (X″X) and that males and
females would be produced in equal numbers. This would
apparently require the assumption that eggs receiving X″
develop into females and those receiving X develop into
males. Thus the factors influencing chromosome elimi-
nation would be effective after, rather than before, matu-
ration of the egg. To account for the variable sex ratio
on this basis alone it would be necessary to assume that
segregation of X″ and X in the egg is not random, that in
some females one and in some the other tends to be re-
tained in the egg rather than to go off in the polar body.
These considerations are presented more to indicate the
nature of the evidence and the problem than as an expla-
nation. One fact recently ascertained (unpublished) may
have special bearing on the problem. It is that in *S. ocel-
laris,* a species giving both bisexual and "unisexual"
families, more crossing over has been found between the
sex chromosomes than was found in *S. coprophila* (Smith-
Stocking, 1936) where families are regularly "unisexual."
This may permit crossing over of influential genes be-
tween X″ and X and give chromosomes of different
"strengths," which in turn might account for the variable
sex ratios.

In *S. coprophila* a strain giving bisexual families arose
in the laboratory by mutation from one of the standard
"unisexual family" strains (Metz, 1931b). For a time it
appeared that analysis of this strain might explain con-
ditions in all strains or species giving bisexual families,
but it was soon found that the females giving bisexual
families in this strain all had an extra X chromosome and
represent a special case not comparable to the others.
Apparently a mutant gene is present in one X chromo-
some which is responsible for retention of the triplo-X
condition in some females (Reynolds, in press).

Selective Types of Chromosome Behavior and the Mechanism of Mitosis

From the cytological standpoint three aspects of chro-

mosome behavior in Sciara have special interest. One is
the monocentric first spermatocyte mitosis, another the
behavior of the "precocious" chromosome in the second
spermatocyte, and the third the selective elimination of
chromosomes during cleavage. These have been dis-
cussed in some detail previously (Metz, Moses and Hoppe,
1926; Metz, 1933, 1936; DuBois, 1933).

The fact that in the monocentric (unipolar) mitosis
homologous chromosomes segregate accurately without
synapsis, without alignment on a metaphase plate, and
when oriented with respect to only one pole, reveals an
unexpected specificity or autonomy of movement on the
part of chromosomes and indicates that the widely dis-
tributed processes of synapsis, metaphase alignment, etc.,
are not essential for accurate segregation (although they
may be for random segregation). Similarly, the fact that
maternal chromosomes segregate from their paternal
homologues as a group and that the two groups respond
in an opposite and predetermined manner in the unipolar
field (one going regularly to the pole while the other goes
away from it) indicates that segregation and movement
here are not dependent on genic homology, but on some
apparently general characteristic imparted by the sex of
the parent. The specificity of this influence is indicated
by the fact already noted that the same chromosomes
which go to the pole in one generation, where they are of
maternal derivation, will do just the opposite and pass
away from the pole in the next generation (of males)
because now they are paternal in origin.

It has been considered a well-established principle that
in mitosis accurate segregation or movement of chromo-
somes into two groups requires a bipolar or multipolar
field. The monocentric mitosis in Sciara, however, shows
that this is not the case. This provides further indica-
tion that chromosome movement involves a much larger
element of autonomy than was formerly supposed. Spe-
cial interest attaches to the movement of chromosomes
which retreat from the pole instead of going toward it.

These show by their orientation, shape and proximal attenuation that a force is being exerted on (or by) them in the direction of the pole. Yet in spite of this they move in the opposite direction. Such movement reveals the activity of another and opposing force. The former force coincides in direction and influence with the "spindle fibers," and its activity is centered at the point of attachment of the "fiber" to a chromosome. The latter force, however, is distinctly different in manifestation, and presumably in nature (Metz, Moses and Hoppe, 1926; Metz, 1933, 1936). It apparently acts on, or is an activity of, the entire chromosome or something distributed through the chromosome, not localized at the one point. Thus this monocentric mitosis serves to indicate the presence of two distinct forces influencing chromosome movement in mitosis. It seems reasonable to assume that these are ordinarily present in the usual type of mitosis elsewhere, but are indistinguishable there because of the nature of the figure.

The movement of the "precocious" chromosome in the second spermatocyte mitosis is similarly significant. This chromosome moves to one predetermined pole before any of the other chromosomes move poleward; and both sister halves move together, even though, in the later stages at least, one is "attached" to a spindle fiber extending toward the opposite pole (Metz, Moses and Hoppe, 1926; Metz, 1936). Like the behavior in the monocentric mitosis, this process serves to limit the possibilities in formulating any general interpretation of the mechanism of mitosis. It shows, for example, that migration of chromosomes to the poles can not be explained primarily by repulsion of chromosomes moving in opposite directions, or by elongation of an interzonal spindle in anaphase, and it is difficult to see how it could be due to an independent system of currents in the spindle—to cite the basic principles of three well-known hypotheses. The process again serves to emphasize the probability that chromosomes take an active part in their own movements rather

than merely responding passively to external agents (Metz, 1936).

The phenomena of chromosome elimination are of interest especially from the standpoint of individual specificity. Like the activity of the "precocious" chromosome they are manifest only by certain particular chromosomes, even though the others are subjected to the same influences. In the process of elimination the particular chromosome to be eliminated appears first to have its activity slowed down—presumably by some outside influence in the cytoplasm. Its transformation from prophase to metaphase seems to be delayed (Metz, unpublished). From metaphase through anaphase it apparently can not keep pace with its fellows, and consequently its daughter halves do not reach the poles to be included in the daughter nuclei. Activity is not entirely inhibited, however, for as already indicated, the eliminated chromosomes may go through subsequent transformations almost in step with those in the nuclei for one or perhaps two cell generations. It seems evident that something in the particular chromosome is influenced by an external agent to cause the inhibition.

From this standpoint the most interesting and puzzling feature is the elimination of one sister derivative of the "precocious" chromosome without the other, as already noted (p. 507). Since chromosome elimination occurs as the nuclei move out from the center toward the periphery of the egg, it has been suggested (DuBois, 1933) that the cytoplasm of the egg is stratified and that elimination is caused by specific properties of particular layers of cytoplasm through which the nuclei pass. It seems equally probable, however, that it may be due to progressive changes occurring throughout the egg (except in the separated germinal region at one end) and would take place if the nuclei remained near the center. Experiments have been designed to test this possibility, but not yet carried out.

Conclusion and Summary

In conclusion it should be emphasized that aside from the minor differences noted, the cytological and genetic peculiarities considered in the present account are for the most part characteristic of all species of Sciara studied. This means that the condition as a whole has become established in a large group of species, but the range of modifications already found indicate that stability has not yet been reached.

Since this account is itself a summary no attempt will be made to summarize it more than is done in the preliminary outline on page 487 and in Figs. 1 and 2.

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WAS THERE AN ARCHATLANTIS?

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THREE years ago Dr. René Jeannel (1935) published an interesting paper on "Archatlantis," a supposed Tertiary land bridge connecting the lands about the Mediterranean Sea with the West Indies and Central America. This bridge was not original with Jeannel, but he cited new evidence for it, drawn from the distribution of three genera of beetles of the family Carabidae. I wish here to review the evidence of the Carabidae (I am myself a specialist in this family), and then to examine critically some other evidence which has been cited for a land bridge from the Old World to the West Indies.

I am indebted to Dr. Thomas Barbour for reading the manuscript of this paper and for useful criticisms.

Three unrelated genera of Carabidae are especially stressed by Jeannel. The first, Stylulus Schauf. (Petrocharis Ehlers) of the tribe Anillini (Jeannel, 1937), is known *only* from three species in Algeria and Tunis and one on St. Thomas in the Virgin Islands in the West Indies. The second genus, Limnastis of the tribe Limnastini, is found in most of the warmer parts of the Old World, including the Mediterranean region and the Canary Islands, but in the New World is known only from one species confined to Cuba and a second which occurs in both Cuba and Guatemala. Finally, the genus Perileptus of the tribe Perileptini is widely distributed in the Old World, including the Mediterranean region, and occurs upon both the Canary and the Cape Verde Islands, but in America is found only on the Greater Antilles, the four big islands of the West Indies. There are four distinct species of Perileptus on the Greater Antilles, and they are most closely related to *Perileptus nigritulus* Woll. of the Canaries. No other species of the whole tribe Perileptini is known anywhere else in the New World.

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There can be no question about the relationships of the species of these three genera. The groups to which they belong have all been ably monographed for the whole world by Dr. Jeannel. The ranges of some of the genera may be extended by future discoveries, but that will not affect the close relationship of the West Indian and Mediterranean species.

I had better say at once that I agree with Dr. Jeannel that the distribution of these forms and the closeness of their relationships indicate direct dispersal from the Old World to the West Indies. I do not, however, agree that this requires a land connection. To see why a land connection is not needed, it is necessary to examine the characteristics of the three genera more closely.

So far as their habits and adaptations go, these three genera have little in common. Stylulus is blind and flightless, and is more or less subterranean; the West Indian Limnastis and Perileptus have eyes and can fly,[1] and they live on or near the surface of the ground. Perileptus is *strictly* associated with rapid streams, Stylulus and Limnastis are not. If these three genera all reached the West Indies over a land bridge, the bridge was substantial enough to have streams of fresh water and lasted long enough for the minute, blind, flightless Stylulus to cross. The whole tribe to which Stylulus belongs is blind and flightless; it is as certain as such a thing can be that the genus was not distributed by winged ancestors. If a land bridge really existed which could carry both Stylulus and Perileptus to the West Indies, there ought to be many other animals, even vertebrates, showing close relationships between the Mediterranean region and the West Indies and occurring on the Atlantic islands. But, as I shall point out below, the most significant terrestrial vertebrates do not show such relationships.

Although the three genera of Carabidae are so dissimilar in habits and adaptations, they do share one sig-

[1] Perileptus is probably always functionally winged. *Limnastis americanus* Darl. has dimorphic wings, but long-winged individuals can fly; I have seen one fly to light at the Soledad Laboratory, Cuba.

nificant characteristic. All are very small. *Stylulus nasutus* Schauf. (*Petrocharis eggersi* Ehlers) is only 0.8 mm long, and is the smallest of West Indian Carabidae. *Limnastis capito* Bates is barely over 1 mm, and is the second smallest Carabid known from the West Indies. (*L. americanus* Darl. is slightly larger, about 1.5 mm). The smallest West Indian Perileptus, *minutus* Darl., measures 1.7 to 1.8 mm; it is not actually the third smallest West Indian Carabid, but is a close runner-up. (The other three West Indian Perileptus are somewhat larger, 2.5 to 3.0 mm, more or less.)

According to a list which I have in manuscript, there are more than 60 genera and some 314 species of Carabidae known from the West Indies, exclusive of Trinidad. Is it not remarkable that, out of this number, the three genera and (by latest count) seven species which Jeannel has found to show such close relationships with the Mediterranean region include the two smallest West Indian Carabidae and another which is close to being the third smallest and that such minute forms occur in all three genera? This would be an extraordinary coincidence if these insects really reached the West Indies by land, but it would not be so surprising if they came through the air, and I believe that this is the real explanation of the presence of these minute beetles in the West Indies.

There is really a surprising amount of evidence pointing to aerial dispersal of these insects. The small size is very significant. Since the volume and weight of an animal vary as the *cube* of its length, while the area of body surface varies only as the *square,* a beetle one millimeter long has about 24 times as much surface for its weight as a beetle one inch long, and is correspondingly more likely to be carried by winds. I know from sad experience that even light air currents, such as those set up by ordinary breathing, are enough to blow such minute insects away.

The details of distribution and the direction of migration are significant. All three genera occur in the northwest coastal region of Africa, and two of them also on

islands off the coast—Perileptus, on both the Canary and
Cape Verde Islands; Limnastis, on the Canaries.[2] More-
over, all three genera seem to have crossed the Atlantic
from east to west, from Africa to the West Indies. This
distribution and direction of migration agree as exactly
as possible with the course of the prevailing winds. The
trades blow from near the northwestern coast of Africa
south and west to the West Indies, and hurricanes fre-
quently originate near the Cape Verde Islands and move
directly to the West Indies. Moreover, there are local
storms called "harmatans" which blow from Africa to
the Cape Verde Islands. The close correlation between
the range of, for example, Perileptus and the course of
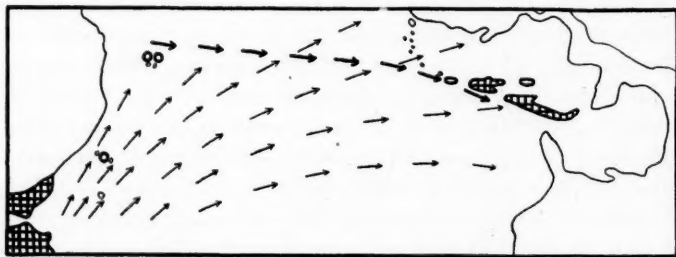the trades and hurricanes of the Atlantic is shown in
Fig. 1.

Fig. 1. Approximate course of summer trade winds at sea level (light
arrows) and path frequently followed, with variations, by hurricanes from
the Cape Verde Islands to the West Indies (heavy arrows) (after Tannehill,
1934); and distribution of genus Perileptus in western Mediterranean region,
the Canary and Cape Verde Islands, and the West Indies (after Jeannel,
1935; distribution in the West Indies extended to include recent discoveries).

The trades, of course, are not merely horizontal winds,
but feed into a zone of rising air which extends all the
way across the Atlantic, and at an altitude of a few thou-
sand feet they blow even more directly from Africa to the
West Indies than they do at sea level.[3] And a hurricane

[2] The distribution of these minute forms is still far from completely
known. It is quite possible that Limnastis will be found on the Cape Verde
Islands as well as on the Canaries, and that Stylulus will turn up on one or
both groups of islands too.

[3] According to a letter (July 8, 1937) from Professor C. F. Brooks, of

is not a random system of winds, but a natural engine driven by an immense volume of rising air near the center of the storm.   Objects of the proper weight might be carried up by the inner, ascending winds of a hurricane and thrown out high at one side, to settle gradually into the lower, incurving winds and be carried to the center again, and this cycle might be repeated many times.   It is possible that a small amount of very light plant debris is sometimes carried from northwestern Africa or from the islands off the African coast to the West Indies by trade or hurricane winds, and, if so, the minute Carabidae described above are the sorts of insects most likely to be carried along.   Some of them are small enough to hide in a crack in the petiole of a small leaf.   They might be carried free in the air for long distances, even without flying.   They are not so very many times larger than some of the particles we see in bars of sunlight, carried about by the almost imperceptible air currents in an occupied room.   The insects would not float in a room, of course, but a very light ascending breeze could carry them.

As to the distances which winds carry insects, Visher (1925) says that Professor F. Wood Jones has observed hundreds of dragonflies arriving at Cocos-Keeling Island during northwesterly gales associated with hurricanes. The nearest land from which they could have come was Sumatra or Java, about 700 miles away.   Certain crop pests are thought to have been brought to Cocos-Keeling

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Harvard, the trade winds in the northern hemisphere turn more and more to the right with increasing height until, at about 1,500 feet altitude, they are around 30° to 45° to the right of the surface direction.   From 1,500 to 5,000 or 10,000 feet altitude there is little change in direction, but higher than that the trades virtually reverse and form what are commonly called the anti-trades.   This description holds also in a general way for the trade winds of the southern hemisphere, except that rotation is to the left with increasing height.   This rotation must be taken into account in dealing with dispersal of organisms by trade winds, for organisms which are carried very far are likely also to be carried high.   It should be remembered, too, that, generally speaking, high altitude winds the world over move very much faster than winds near the ground.

by the same winds, too. However, 700 miles is not very far compared to the distance from Africa to the West Indies. From the Cape Verde Islands to the West Indies is more than 2,000 miles; from the Canary Islands or the coast of Africa, still farther. This is a very long distance, but no longer than that from North America to the Hawaiian Islands. It is true that the latter are not so isolated on the west, but nevertheless, if one believes, as some zoologists do (for example, Perkins, 1913, in the introduction to *Fauna Hawaiiensis,* pp. lii–lxi; and Gulick, 1932), that the insects of the Hawaiian Islands are descended from a few ancestors which somehow crossed the ocean from various directions, it is easy to believe too that a few very minute insects have crossed the Atlantic directly to the West Indies. It is, I think, very significant that, among the few stocks of Carabidae which have reached the Hawaiian Islands, are two of the same three groups which show such close African-West Indian relationships. For the Hawaiian *Typhlonesiotes swaluwenbergi* Jeannel (1937, p. 325) is a species of the Anillini 0.8 mm long, and a species of Limnastis (*swaluwenbergi* Jeannel, 1932, p. 176) also occurs in the Hawaiian Islands. Only the Perileptini are unrepresented. The suggestion that certain minute insects have been carried enormous distances over oceans by winds agrees extremely well with Gulick (1932), who finds evidence that certain minute land snails, of which the adults are of the order of one millimeter long, have been carried by winds to even the most remote oceanic islands.

To sum up, the three genera of Carabidae which Jeannel has found to show such striking African-West Indian relationships are precisely those minute forms most likely to be carried through the air. The small size of all three is an extraordinary coincidence unless dispersal has been by air. The details of distribution of the genera and the apparent direction of migration, from east to west, are exactly what would be expected if dispersal has been by trade or hurricane winds. And two of the three groups

have somehow reached such an isolated spot as the Hawaiian Islands, which suggests that they have some great power of dispersal. Surely this is a pretty good case for aerial dispersal.

If aerial dispersal of minute organisms directly from Africa to the West Indies really has occurred, other examples should turn up, not only among insects, but among small spiders and other minute forms of life. Probably the microfauna of the islands is not yet sufficiently well known to show whether many examples exist. Petrunkevitch (1928) has remarked that he knows of none among West Indian spiders.

Except for the Carabidae discussed above, most of the evidence for a Mediterranean-West Indian land bridge is so old as to be almost traditional, and is usually cited uncritically by modern zoogeographers. This is unfortunate, for critical examination in the light of recent knowledge shows that the evidence is not quite what it has been supposed to be. Since it is impossible in the present short paper to discuss the evidence of all groups of animals, I shall consider in detail only a few of the most significant groups, arbitrarily eliminating those of doubtful significance.

Among the animals of very doubtful significance in connection with land bridges are all sorts of water-living marine animals. Land bridges ought to be shown by land animals, and if the land animals do not show a bridge, arguments drawn from water-living forms will not make the bridge seem very probable. This is true not only of marine invertebrates, but of the vertebrate Sirenians. Nobody really knows how wide an ocean gap Sirenians are able to cross, and even if they have followed a coast line across the Atlantic, the coast line need not necessarily have led directly from the Mediterranean region to the West Indies.

Insects, too, are very unreliable sources of evidence about land bridges. Their powers of dispersal are too great and their fossil history is too little known. The evi-

dence of land mollusks is probably somewhat more reliable, but is still far from satisfactory. So many land snails have reached remote oceanic islands that we are compelled to believe that they are sometimes able to cross wide ocean gaps. Moreover, in the case of the Mediterranean-West Indian bridge, the evidence of the land mollusks is disputed among malacologists. Scharff and others, by citing only a few very carefully selected examples, have tried to wring out evidence in favor of the bridge, but Pilsbry (1911, pp. 615, 620–621, 625–626) believes that the tropical American mollusk fauna as a whole shows no real evidence of a transatlantic land bridge via the West Indies, although he does believe that there was a more southern land connection between Africa and South America.

There is, of course, plenty of room for differences of opinion about the zoogeographic significance of marine animals, of insects and of land mollusks, but most persons would probably agree that terrestrial vertebrates give the best evidence for or against land bridges. Terrestrial vertebrates disperse readily over land but hardly at all over wide ocean barriers, and the fossil history of at least some of them is relatively well known. It ought to be possible to decide from the evidence of terrestrial vertebrates alone whether or not any given Tertiary land bridge really existed. Among West Indian terrestrial vertebrates which have been cited as evidence of a transatlantic bridge are the mammal Solenodon, a snake of the genus Natrix, lizards of the family Anguidae, and the Salamander Spelerpes.

It seems to be agreed that Solenodon, found in Cuba and Hispaniola, has its closest *living* relative in Centetes of Madagascar. However, the relationship is not really very close. The two genera are placed in different families. According to Romer (1933, pp. 271–272) related fossil forms are known from the early Tertiary of North America, and Scott (1937, p. 152) says that Solenodon and Centetes are "almost the last surviving relics of an

ancient group that was nearly world-wide in distribution.'' In view of these statements by paleontologists, Solenodon can not very well be considered evidence for a land bridge direct from Africa to the West Indies.

Natrix (= Tropidonotus; Scharff, 1912, pp. 128–129, 222) occurs on every continent except South America. In the West Indies, however, the genus is found only on Cuba. The single Cuban species is now known to be the same as *Natrix compressicauda* (Kennicott) of southern Florida, and is believed to be a recent immigrant from Florida into Cuba (Barbour and Ramsden, 1919, pp. 212–213). Natrix, then, although it links North America and the Old World, does not suggest a West Indian land bridge, nor do any related genera indicate such a bridge. (For information about Natrix, and about the Anguidae and Spelerpes below, I am indebted to Mr. Arthur Loveridge and Mr. Benjamin Shreve.)

As for the Anguid lizards cited by Scharff (1912, p. 281), only one genus of the family (Ophisaurus) occurs in both the Old and the New Worlds. It is found in Europe and North America, but *not* in the West Indies. The West Indian members of the family belong to other genera which appear to show no direct relationship with Old World forms. Living Anguids, then, like Natrix, show a closer relationship between North America and Europe than between the West Indies and Europe. Add to this that fossil Anguidae are known from the Tertiary of both Europe and North America (according to Arldt, 1919, p. 209), but again *not* from the West Indies, and it will be seen how little these lizards really indicate a land bridge by way of the islands.

Finally, the genus Spelerpes was formerly supposed to occur in Mexico, Haiti, and Europe. Now, however, the European species are put in the genus Hydromantes, which occurs in the New World only in California—a remarkable distribution, but one which has nothing to do with the West Indies. Dunn (1926) in his revision of the Plethodontidae, the family to which Spelerpes belongs,

suggests (p. 32) that *Spelerpes infuscatus* of Haiti had an
incorrect locality label and was not really from the West
Indies at all.   Dunn says further that, even if the species
were Haitian, it would not indicate a land bridge from
Europe to the West Indies.   Dunn, in fact, finds no diffi-
culty in accounting for the distribution of the whole
family Plethodontidae by dispersal through the north.
His map on page 2 is especially interesting.

The four groups of vertebrates discussed above do
occur in the West Indies, or at least have been supposed
to occur there.   Even this can not be said for some other
vertebrates which have been cited for a West Indian land
bridge.   For example, the tortoise genus Clemmys
(Scharff, p. 222) does not occur in the West Indies and
has no relatives there, and the same is true of the voles
and hares (Scharff, pp. 223–226).   Yet Scharff would
account for the distribution of all these groups by dis-
persal via the islands.   Joleaud (1919) cites certain fossil
horses as evidence of a land bridge from the Old World
to the West Indies and Florida, although no trace of
native horses, living or fossil, has ever been found on the
West Indies.   And Scharff (pp. 204–205, 220–221) tries
to explain the distribution of Pelobatidae (spade-foot
toads) by dispersal across a West Indian land bridge, and
would account for the presence of a species on Martha's
Vineyard (a small island, recently derived from the
coastal plain, a few miles off the coast of Massachusetts)
by a bridge from the West Indies through Bermuda—all
in spite of the fact that no Pelobatidae have been found
anywhere in the West Indies or on Bermuda!   This prob-
ably sets a world's record for unnecessary land bridges.
These are interesting examples of the lengths to which
some zoogeographers will go to find "evidence" for their
favorite bridges, but they obviously have no real bearing
on the existence or non-existence of a transatlantic bridge.

To return to the four groups of vertebrates which really
occur (or have been supposed to occur) in the West
Indies, it has been found that no one of them really re-

flects dispersal across a mid-atlantic bridge. On the contrary, in the opinion of persons competent to judge, every one of the groups shows evidence[4] of dispersal through the north. Not a single one of these groups of terrestrial vertebrates gives real evidence of a transatlantic migration such as seems to have occurred among Carabid beetles.

Probably the adverse evidence of any one of these groups of animals could be reconciled with the existence of a West Indian land bridge if there were better evidence to show that the bridge really existed, but, so far as I can find, there is no better evidence. The examples discussed above are the best that zoogeographers have been able to find among the most significant animals, the terrestrial vertebrates.[5] Scharff, to whose specious reasoning we owe several land bridges which really never existed, admits (pp. 280–281) that, "Among the terrestrial species of vertebrates and invertebrates of the Antilles, as I observed, the affinity with Europe is less marked perhaps than it is in the south-western States of North America." In other words, the terrestrial fauna as a whole shows a closer connection between the southwestern United States and Europe than between the West Indies and Europe. The history of Archatlantis has been the history of an attempt to twist this embarrassing state of affairs into evidence that there has been migration from Europe through the West Indies to Mexico and the southwestern

[4] Since this was written, Mr. Benjamin Shreve has called my attention to Tarentola, a genus of Gekkonid lizards. The species of the genus occur in western Africa, the borders of the Mediterranean Sea, Madeira, and the Cape Verde Islands, and there is also a single species in the New World, on Cuba and some of the Bahama Islands. This extraordinary distribution seems never to have received the thorough study which it deserves.

[5] I have not mentioned a few groups of vertebrates, like the snake family Boidae, which occur in the Old World and the West Indies and which are widely distributed also in South America. These groups may or may not have been dispersed originally through the northern hemisphere. If not, they probably reached South America direct from Africa, not by way of the West Indies, for there is a good deal of evidence (much too complex to be given here) that a direct land connection once existed between Africa and South America.

states.   The examples from terrestrial vertebrates cited
above are fair examples of the lengths to which the twist-
ing and forcing of evidence have been carried.   It seems
to me that Jeannel is the only author who has found real
evidence of a direct transatlantic migration of land ani-
mals from the Old World to the West Indies, and, as I
have tried to show, there are very good reasons for believ-
ing that Jeannel's beetles came through the air rather
than over land.   The contrast between the present distri-
bution of these beetles and the distribution of flightless
land vertebrates is additional evidence that the insects
have been dispersed through the air.

There is, in fact, so far as I have been able to find, no
real zoological evidence that there ever was a land bridge
between the Old World and the West Indies.   And
Schuchert (1935), in his recent "Historical Geology of the
Antillean-Caribbean Region," concludes (pp. 42–43) that
there is no geological evidence of such a connection.
There may perhaps have been a land connection farther
south, between Africa and South America, but the evi-
dence is clear that there has been none by way of the West
Indies.   In this sense, there was no Archatlantis.

Summary

The distribution of three genera of beetles of the family
Carabidae has been cited by Jeannel as evidence of a
Tertiary land bridge (Archatlantis) connecting the lands
about the Mediterranean Sea with the West Indies.   The
beetles, however, do not really give evidence of such a
land bridge.   The three genera are all exceptionally
minute and all seem to have crossed the Atlantic from
east to west, the direction of both trade winds and hurri-
canes.   These facts indicate that the beetles have not mi-
grated over a land bridge but have been carried across the
Atlantic by winds.   The fact that two of the three genera
have relatives on the remote Hawaiian Islands is a
further indication that they are capable of dispersal by
winds.   Terrestrial vertebrates, the most significant of

all animals where land bridges are concerned, show no sign of a bridge from the Old World to the West Indies, and there seems to be no geological evidence that such a bridge has existed. It is concluded that the three genera of Carabidae have been carried across the Atlantic by winds, that there was no Tertiary land bridge from the Old World to the West Indies, and that in this sense there was no Archatlantis.

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A HANDLIST OF AMERICAN NATURALISTS, BASED ON THE DICTIONARY OF AMERICAN BIOGRAPHY

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WITH the publication in 1936 of the twentieth and final volume of the Dictionary of American Biography,[1] under the auspices of the American Council of Learned Societies, there was brought to completion probably the greatest piece of biographical research ever undertaken in this country. There is nothing else that approaches it in completeness, scholarly treatment and scope. It is a generous cross section of American endeavor, and it will be the standard reference work in its field for many decades to come.

An old rhyme classifies mankind as—

> Rich man, poor man, beggar man, thief,
> Doctor, lawyer, merchant, chief.

All of them are included in the Dictionary of American Biography, the main requisite being that they must have attained an eminence of sufficient stability to meet the standards of the editors. They must have made "some significant contribution to American life in its manifold aspects." Nor was any living person included.

The editors have been liberal but discriminating and impartial in their long task, and have thereby produced volumes that are exceedingly alive. In using them, in fact, one has difficulty in reading only what he may be looking up at the time. You may be wanting only the birthday of, say, Commodore Preble, but before you know it you are deep in the life of Daniel Pratt (1809–1887), vagrant; or John Quelch (1665–1704), pirate; or Red Wing (1750–1825), Sioux chief; or perhaps some Revolutionary saddle and harness maker. You will find Johnny Appleseed as well as Abraham Lincoln. Hernando

[1] Charles Scribner's Sons, New York.

DeSoto, famed conquistador and discoverer of the Mississippi River, is there, and so is Edward Payson Weston (1839–1929), long-distance walker; Carry Nation and Sacco and Vanzetti. There is no accounting for fame, and famous Americans are an interesting lot.

"So far as knowledge permits the Dictionary has endeavored to re-create or re-interpret the lives of the makers of American life and culture." Through the 13,633 biographies by which this aim has been accomplished, the name of science looms large. America may well boast of the large number of scientists who have attained not only national but world-wide distinction. And if there is a basic, undercurrent interest that has inspired American scientists as a whole, it is the study of natural history. This is because of nature's many-faceted appeal for both the professional and the amateur. "Nature," says Alan Devoe, "is a matter of chemical fusings and mathematical formulae and biological permutations. But nature is also the singing of phoebes in country meadows in the spring, and the leap of catfish in rush-ringed ponds, and an exultation and a miracle."

One of the frequent contributors to the earlier volumes of the dictionary, Donald Culross Peattie, writes in his book "Green Laurels": "Of all things under the sun that a man may love, the living world he loves most purely. In a lifetime's devotion to it there is no self-interest." Because this American love of nature has been a passionate one, it has become a pervasive influence, not only in the sciences but also in the arts and in literature. "Except for the New England passion for ideals, Whitman's passion for democracy, and Poe's lovely devotion to beauty, I sometimes think," says Dr. H. S. Canby, former editor of the *Saturday Review of Literature,* "that this is the only great passion that has found its way into American literature."

The purpose of the accompanying list of American naturalists is merely to assemble them for convenient reference and to make more easily apparent any significance

that they may have as a whole. I have included only the names of those whose biographies appear in the Dictionary of American Biography. The designation "naturalist" has been interpreted rather broadly, to embrace any person who in any reasonable sense could be considered to have contributed to the science or advancement of natural history. A preeminent teacher of biology or geology, for example, might not strictly be considered a naturalist, but in the wider sense, because of his influence and basic indispensability, he can make significant, though perhaps intangible, contributions to natural history. In other words, I have included the indoor as well as the outdoor naturalist, for each is a necessary complement of the other. In many cases, of course, both kinds have been fortunately combined in one man, and when that occurs we have a naturalist par excellence. That is what makes William Brewster, for instance, a greater naturalist than Thoreau or Burroughs or than many a "closet" naturalist that could be named.

Paleontologists (but not purely economic and physical geologists) are included, for in so far as geology is the study of the past life of the earth as recorded in the rocks and utilizes the principles of zoology and botany, it is the very essence of natural history. We may well believe, with Alfred Noyes, that—

> These rocks, these bones, these fossil forms and shells
> Shall yet be touched with beauty and reveal
> The secrets of the book of earth to man.

Likewise, horticulturists are included if there is any indication in their biographies that their interest in plants was appreciably more than economic, if there was any "naturalist blood" in them at all. The line in some cases is hard to draw. To try to draw it too closely would be to invalidate the history of science itself, for we must remember, as Mr. Peattie, again, has said, that "ultimate progress sprang from the most unpredictable of all little buds of the tree of science. Out of superstition grew the science of botany. Though to-day this sober subject proceeds on

its way respected, undeviating, confident of further triumphs, if it looks back, it must thank the old herbgatherers, and the herbalists scratching compendiums of misinformation upon parchment.''

There need be no other test of the quality of these naturalists' biographies than that of the biographers themselves. Many of them are eminent naturalists in their own right and so are especially qualified to write of the departed heroes of their own fields. Dr. Leland Ossian Howard, veteran entomologist and for many years chief of the Federal Bureau of Entomology, has written most of the entomologists' accounts; Dr. Witmer Stone, of the Academy of Natural Sciences of Philadelphia, many of the ornithologists'; Dr. George Perkins Merrill, late mineralogist of the United States National Museum, the geologists' (he wrote more than 70 for the whole dictionary); et cetera. Some of the biographers themselves have now passed on, notably Dr. David Starr Jordan, Dr. George Perkins Merrill, Dr. Marcus Benjamin, Dr. Barton Warren Evermann, Dr. Walter Hough—the first two mentioned in time to take their own places close to the names of those whose lives they had but recently recapitulated.

Names of many naturalists come at once to mind who have died since the volume was published in which they would have appeared: Dr. Edward William Nelson, Dr. Amos Butler, Dr. Frederick Vernon Coville, Dr. William Jacob Holland, Dr. David White, Dr. William Temple Hornaday, to name but a few. But theirs is another chapter, separated only fortuitously from that of their contemporaries. It is hoped that supplements to the dictionary are to be published, as was done in the case of the (English) Dictionary of National Biography, to correct the matter of necessary but arbitrary dead-lines.

It is beyond our purpose here to suggest that certain naturalists should or should not have been included in the dictionary. To do so would be to presuppose as thorough an inquisition by ourselves as that conducted by the dictionary editors. Naturally there are names that we miss,

but, remembering that it was prescribed that "the Dictionary cannot find a place for average or merely typical figures, however estimable they may be," we believe that the editors have done an excellent and praiseworthy job. As for the present list, it may be considered an answer to the question: "Who were the 375 [odd] greatest American naturalists?" It covers a period of approximately 300 years (1622–1933).

Finally, in compiling this roster of distinguished naturalists, I have been greatly impressed by the spirit that has moved them forward in their devotion to nature. It is a kind of patriotism to the natural world, more inspiring and transcendent, more moving and admirable than is the patriotism to one's country. It is everything that is meant by "love of nature," and it is found in all degrees and manifestations. One man may use a microscope, another a camera, another his ear and naked eye to search out the unfathomable secrets of nature, but each is satisfied, though often mystified, by the rich return that nature gives, for, as Wordsworth was inspired to write, "Nature never did betray the heart that loved her." It was voiced a century and more ago in William Cullen Bryant's great nature hymn "Thanatopsis." I have found it more recently memorably expressed by Dr. Erwin F. Smith in a tribute[1] to "W. E. S." (William Edwin Safford; see list), which may be taken as a composite salute to all American naturalists:

> Within his soul, as in a Buddhist shrine
> The god, a gentle Nature-Worship, glowed;
> He saw upon Earth's face where'er he strode
> Footprints of God and finger-marks divine.
> The breath of peace in lily, palm, and pine,
> The long allurement of the open road,
> By suns and winds and waters overflowed,
> Were more to him, entranced, than bread or wine.
>
> He heard in Nature voices manifold;
> Beyond the known he seemed to catch faint gleams
> Of deeper and diviner things untold;
> Therefore, the hills sang to him and the streams,
> The dross of other men became his gold,
> And all his days were full of wistful dreams.

[1] Official Record, U. S. Department of Agriculture, Jan. 20, 1926.

The matter placed in brackets in the third column under "Designation" has been added by me as further explanation of the various naturalists' fields of endeavor. All other data are recorded as given in the dictionary. Readers are referred to the forewords to volumes 1 and 20 of the dictionary and to the index to volumes 1–4 for statistical material regarding the work and for further description of its purposes, scope and sponsorship.

Though it is difficult to classify the naturalists, since many of them were specialists in several fields, the following classification of the 378 names in the list will show in a general way how they are divided among the various branches of natural history:

Zoological sciences	116
Botanical sciences	107
Geological sciences	66
General	70
All others	19
Total	378

Name	Dates	Designation	Biographer
Abbott, Charles Conrad..	1843–1919	Naturalist, archeologist, author.	Witmer Stone.
Adams, Charles Baker ..	1814–1853	Naturalist, [conchologist].	H. A. Pilsbry.
Agassiz, Alexander	1835–1910	Zoologist, oceanographer, mine operator.	D. C. Peattie.
Agassiz, Jean Louis Rodolphe	1807–1873	[Geologist, zoologist].	David Starr Jordan, Jessie K. Jordan.
Akeley, Carl Ethan	1864–1926	Taxidermist, inventor, naturalist, explorer.	G. Clyde Fisher.
Allen, Joel Asaph	1838–1921	Zoologist, author, [ornithologist, mammalogist].	H. F. Osborn.
Allen, Timothy Field	1837–1902	Physician, botanist.	H. L. Clark.
Anthony, John Gould ...	1804–1877	Zoologist, [conchologist].	H. A. Pilsbry.
Ashmead, William Harris	1855–1908	Entomologist.	L. O. Howard.
Atkinson, George Francis	1854–1918	Botanist.	D. C. Peattie.
Audubon, John James ..	1785–1851	Artist, ornithologist, naturalist.	D. C. Peattie. Eleanor R. Dobson.
Bachman, John	1790–1874	Naturalist, Lutheran clergyman.	D. C. Peattie.
Bailey, Jacob Whitman..	1811–1857	Botanist, chemist, geologist.	Stanley Coulter.
Baird, Spencer Fullerton	1823–1888	Zoologist.	D. S. Jordan, Jessie K. Jordan.
Baldwin, William	1779–1819	Physician, botanist.	Henry R. Viets.
Banister, John	1650–1692	Botanist.	A. C. Gordon, Jr.
Barnes, Charles Reid ...	1858–1910	Botanist.	D. C. Peattie.
Barton, Benjamin Smith	1766–1815	Physician, naturalist.	George Blumer.
Barton, William Paul Crillon	1786–1856	Botanist, teacher, naval surgeon.	D. C. Peattie.
Bartram, John	1699–1777	Botanist.	D. C. Peattie.
Bartram, William	1739–1823	Traveler, naturalist.	Lane Cooper.
Beal, William James ...	1833–1924	Botanist, teacher.	D. C. Peattie.
Bean, Tarleton Hoffman.	1846–1916	Ichthyologist.	John F. Fulton.
Beecher, Charles Emerson	1856–1904	Paleontologist.	G. P. Merrill.

Name	Dates	Designation	Biographer
Bessey, Charles Edwin ..	1845–1915	Botanist.	D. C. Peattie.
Bigelow, Jacob	1786–1879	Botanist, physician.	D. C. Peattie.
			John F. Fulton.
Binney, Amos	1803–1847	Zoologist, [conchologist].	H. A. Pilsbry.
Bland, Thomas	1809–1885	Naturalist, [conchologist].	Frank E. Ross.
Boll, Jacob	1828–1880	Geologist, naturalist.	Samuel W. Geiser.
Bolles, Frank	1856–1894	Nature writer.	George H. Genzmer.
Brackenridge, William D.	1810–1893	Botanist.	D. C. Peattie.
Bradley, Frank Howe ...	1838–1879	Geologist, [paleontologist].	G. P. Merrill.
Brainerd, Ezra	1844–1924	Botanist, geologist, educator.	D. C. Peattie.
Brandegee, Townshend Stith	1843–1925	Botanist.	D. C. Peattie.
Brewer, Thomas Mayo ..	1814–1880	Ornithologist, oologist.	Witmer Stone.
Brewer, William Henry .	1828–1910	Scientist, [botanist, geologist].	R. H. Chittenden.
Brewster, William	1851–1919	Ornithologist.	Witmer Stone.
Bridges, Robert	1806–1882	Physician, botanist.	F. R. Packard.
Brooks, William Keith ..	1848–1908	Zoologist.	H. A. Pilsbry.
Buckley, Samuel Botsford	1809–1883	Botanist, field naturalist, [geologist].	T. S. Palmer.
Burbank, Luther	1849–1926	Plant breeder, [botanist].	Vernon L. Kellogg.
Burgess, Edward	1848–1891	Yacht designer, entomologist.	W. J. Ghent.
Burrill, Thomas Jonathan	1839–1916	Botanist, horticulturist.	D. C. Peattie.
Burroughs, John	1837–1921	Author, [naturalist].	Norman Foerster.
Calvin, Samuel	1840–1911	Geologist, [paleontologist].	G. P. Merrill.
Cassin, John	1813–1869	Ornithologist.	Witmer Stone.
Catesby, Mark	1679–1749	Naturalist, traveler.	W. H. B. Court.
Chapman, Alvan Wentworth	1809–1899	Botanist, physician.	D. C. Peattie.
Chapman, Henry Cadwalader	1845–1909	Physician, botanist.	F. R. Packard.
Cist, Jacob	1782–1825	Naturalist, anthracite coal pioneer, inventor.	C. W. Mitman.
Clark, Henry James ...	1826–1873	Zoologist, botanist.	Frederick Tuckerman.
Clark, William Bullock .	1860–1917	Geologist.	G. P. Merrill.
Clarke, John Mason	1857–1925	Paleontologist.	G. P. Merrill.
Claypole, Edward Waller	1835–1901	Geologist, educator, [entomologist].	G. P. Merrill.
Clayton, John	1685–1773	Botanist.	D. C. Peattie.
Colden, Cadwallader	1688–1776	Loyalist, lieutenant-governor of New York, philosopher, scientist, [botanist].	Alice M. Keys.
Colden, Jane	1724–1766	Botanist.	M. P. Smith.
Collins, Frank Shipley ..	1848–1920	Botanist.	D. C. Peattie.
Condon, Thomas	1822–1907	Clergyman, geologist, [paleontologist].	G. H. Genzmer.
Cooper, James Graham..	1830–1902	Naturalist, [ornithologist].	Joseph Grinnell.
Cope, Edward Drinker .	1840–1897	Zoologist, paleontologist.	G. P. Merrill.
Coquillett, Daniel William	1856–1911	Entomologist.	L. O. Howard.
Cory, Charles Barney ..	1857–1921	Ornithologist, author.	Witmer Stone.
Coues, Elliott	1842–1899	Ornithologist.	Witmer Stone.
Coulter, John Merle	1851–1928	Botanist.	C. J. Chamberlain.
Cresson, Ezra Townsend .	1838–1926	Entomologist.	L. O. Howard.
Curtis, Moses Ashley ..	1808–1872	Botanist, minister.	D. C. Peattie.
Dall, William Healey ...	1845–1927	Naturalist, [conchologist].	Marcus Benjamin.
Dana, James Dwight ..	1813–1895	Geologist, zoologist.	G. P. Merrill.
Darby, John	1804–1877	Educator, author, [botanist].	W. J. Chase.
Darlington, William ...	1782–1863	Botanist.	D. C. Peattie.
Davey, John	1846–1923	"Father of tree surgery in America," [botanist].	Wm. B. Shaw.
Dean, Bashford	1867–1928	Zoologist, armor expert, [ichthyologist].	Mary B. Hartt.
DeKay, James Ellsworth	1792–1851	Naturalist, author.	Wm. B. Shaw.
Doubleday, Neltje de Graff	1865–1918	Naturalist.	Gladys Graham.
Downing, Andrew Jackson	1815–1852	Landscape gardener, architect, horticulturist, [botanist].	H. A. Kellar.
Downing, Charles	1802–1885	Pomologist, horticulturist, author, [botanist].	H. A. Kellar.
Dudley, William Russel .	1849–1911	Botanist.	LeRoy Abrams.
Dunbar, William	1749–1810	Planter, scientist.	F. L. Riley.
Durand, Élie Magloire ..	1794–1873	Pharmacist, botanist.	G. H. Genzmer.
Du Simitière, Pierre Eugène	1736–1784	Artist, antiquary, naturalist.	Joseph Jackson.

Name	Dates	Designation	Biographer
Dyar, Harrison Gray ...	1866–1929	Entomologist.	L. O. Howard.
Eaton, Amos	1776–1842	Scientist, educator, [botanist].	G. P. Merrill.
Eaton, Daniel Cady	1834–1895	Botanist.	W. R. Maxon.
Edwards, William Henry	1822–1909	Entomologist.	L. O. Howard.
Eigenmann, Carl H.	1863–1927	Zoologist, educator [ichthyologist].	G. S. Myers.
Elliot, Daniel Giraud ..	1835–1915	Zoologist, [ornithologist].	Witmer Stone.
Elliott, Stephen	1771–1830	Botanist.	A. R. Childs.
Ellis, Job Bicknell	1829–1905	Botanist, mycologist.	C. L. Shear.
Emmons, Ebenezer	1799–1863	Geologist, physician, teacher.	G. P. Merrill.
Engelmann, George	1809–1884	Pioneer meteorologist, physician, botanist.	G. T. Moore.
Farlow, William Gilson..	1844–1919	Botanist.	D. C. Peattie.
Fernald, Charles Henry.	1838–1921	Entomologist, teacher.	L. O. Howard.
Fernow, Bernhard Eduard	1851–1923	Forester, author, teacher.	H. S. Graves.
Fewkes, Jesse Walter ..	1850–1930	Ethnologist, [zoologist].	Walter Hough.
Field, Herbert Haviland..	1868–1921	Zoologist, bibliographer.	H. L. Clark.
Fitch, Asa	1809–1879	Entomologist.	L. O. Howard.
Flagg, Thomas Wilson ..	1805–1884	Naturalist, author.	John D. Wade.
Forbes, Stephen Alfred..	1844–1930	Entomologist, naturalist.	L. O. Howard.
Forbush, Edward Howe .	1858–1929	Ornithologist.	Witmer Stone.
Fuertes, Louis Agassiz .	1874–1927	Artist, naturalist.	A. A. Allen.
Fuller, Andrew S.	1828–1896	Horticulturist, editor.	N. A. Crawford.
Gabb, William More	1839–1878	Paleontologist.	Charles Schuchert.
Garden, Alexander	1730–1791	Naturalist, physician.	D. C. Peattie.
Garman, Samuel	1843–1927	Zoologist, [ichthyologist].	H. L. Clark.
Gibson, William Hamilton	1850–1896	Artist, naturalist.	Catherine P. Mitchell.
Gilbert, Charles Henry ..	1859–1928	Zoologist, [ichthyologist].	D. S. Jordan.
Gilbert, Grove Karl	1843–1918	Geologist, [naturalist].	G. P. Merrill.
Gill, Theodore Nicholas..	1837–1914	Zoologist, "master of taxonomy," [ichthyologist].	D. S. Jordan.
Gillman, Henry	1833–1915	Scientist, U. S. consul, author, [botanist].	Gracie B. Krum.
Girard, Charles Frédéric.	1822–1895	Zoologist, physician.	H. L. Clark.
Glover, Townend	1813–1883	The first man to hold an official entomological position under the U. S. Government.	L. O. Howard.
Godman, John Davidson .	1794–1830	Anatomist, naturalist.	W. S. Miller.
Goff, Emmet Stull	1852–1902	Horticulturist,]botanist[.	J. G. Moore.
Good, Adolphus Clemens	1856–1894	Missionary to Africa, naturalist.	F. T. Persons.
Goodale, George Lincoln.	1839–1923	Botanist, educator.	G. J. Peirce.
Goode, George Brown ..	1851–1896	Naturalist, author, administrator, [ichthyologist].	D. S. Jordan.
Gould, Augustus Addison.	1805–1866	Physician, conchologist.	F. C. Baker.
Gray, Asa	1810–1888	Botanist.	G. H. Genzmer.
Green, Jacob	1790–1841	Teacher, chemist, naturalist.	H. B. Baker.
Green, Samuel Bowdlear.	1859–1910	Horticulturist, educator, [forester].	Solon J. Buck.
Green, Seth	1817–1888	Pioneer fish culturist.	M. C. James.
Greene, Edward Lee	1843–1915	Botanist.	W. L. Jepson.
Grote, Augustus Radcliffe	1841–1903	Entomologist.	L. O. Howard.
Gulick, John Thomas ..	1832–1923	Missionary, naturalist, writer on evolution.	Frederick Tuckerman.
Hagen, Hermann August	1817–1893	Entomologist.	L. O. Howard.
Haldeman, Samuel Steman	1812–1880	Scientist, philologist, [zoologist].	G. C. Harvey.
Hall,, James	1811–1898	Geologist, paleontologist.	G. P. Merrill.
Hallock, Charles	1834–1917	Journalist, author, scientist.	W. G. Bleyer.
Hansen, George	1863–1908	Horticulturist, landscape architect, [botanist].	W. L. Jepson.
Harlan, Richard	1796–1843	Naturalist, physician.	Daniel M. Fisk.
Harris, James Arthur ..	1880–1930	Botanist, biometrician.	R. A. Gortner.
Harris, Thaddeus William	1795–1856	Entomologist, librarian.	L. O. Howard.
Harshberger, John William	1869–1929	Botanist, naturalist, teacher.	H. B. Baker.
Hay, Oliver Perry	1846–1930	Paleontologist.	Richard S. Lull, Nelda E. Wright.
Hayden, Ferdinand Vandiveer	1829–1887	Geologist.	G. P. Merrill.
Heilprin, Angelo	1853–1907	Geologist, paleontologist, explorer, [gazetteer].	Joseph Jackson.
Henderson, Peter	1822–1890	Horticulturist, [botanist].	R. H. Sudds.

Name	Dates	Designation	Biographer
Henshall, James Alexander	1836–1925	Physician. naturalist, writer on angling.	M. C. James.
Henshaw, Henry Wetherbee	1850–1930	Naturalist, ornithologist, ethnologist.	E. A. Goldman.
Herbert, Henry William ["Frank Forester"] ..	1807–1858	Writer, [sportsman].	H. E. Starr.
Herrick, Edward Claudius	1811–1862	Librarian, scientist, [entomologist].	H. E. Starr.
Hildreth, Samuel Prescott	1783–1863	Physician, naturalist, historian.	A. P. Mathews.
Hilgard, Eugene Woldemar	1833–1916	Geologist, [naturalist].	G. P. Merrill.
Hitchcock, Charles Henry	1836–1919	Geologist, [zoologist].	G. P. Merrill.
Hitchcock, Edward	1793–1864	Geologist, educator, clergyman.	G. P. Merrill.
Holbrook, John Edwards	1794–1871	Zoologist, [herpetologist].	H. L. Clark.
Holder, Charles Frederick	1851–1915	Naturalist, sportsman.	W. L. Jepson.
Holder, Joseph Bassett.	1824–1888	Naturalist, physician, author.	Mary B. Hartt.
Horn, George Henry	1840–1897	Entomologist, physician.	L. O. Howard.
Horsfield, Thomas	1773–1859	Explorer, naturalist, physician.	John F. Fulton.
Hough, Franklin Benjamin	1822–1885	Forester, physician.	H. S. Graves.
Houghton, Douglass	1809–1845	Geologist, [surgeon, botanist].	G. P. Merrill.
Howell, Thomas Jefferson	1842–1912	Botanist.	W. L. Jepson.
Hubbard, Henry Guernsey	1850–1899	Entomologist.	L. O. Howard.
Hunter, Walter David ..	1875–1925	Entomologist.	L. O. Howard.
Hyatt, Alpheus	1838–1902	Zoologist, paleontologist.	H. L. Clark.
James, Edwin	1797–1861	Explorer, naturalist, physician.	Frank E. Ross.
James, Thomas Potts ...	1803–1882	Botanist.	Hugh M. Raup.
Jayne, Horace Fort	1859–1913	Biologist.	F. Estelle Wells.
Jordan, David Starr	1851–1931	Naturalist, teacher, university president, peace advocate, [ichthyologist].	B. W. Evermann.
Josselyn, John ......fl.	1638–1675	Traveler, writer.	Fulmer Mood.
Kauffman, Calvin Henry.	1869–1931	Botanist.	J. A. Stevenson.
Kellogg, Albert	1813–1887	Botanist.	W. L. Jepson.
Kemp, James Furman ..	1859–1926	Geologist, mining engineer, [teacher].	G. P. Merrill.
Kennicott, Robert	1835–1866	Naturalist, explorer.	F. C. Baker.
King, Clarence	1842–1901	Geologist, mining engineer, administrator.	G. P. Merrill.
King, Franklin Hiram ..	1848–1911	Agricultural scientist.	W. A. Sumner.
Kirtland, Jared Potter ..	1793–1877	Physician, naturalist, public servant.	F. C. Waite.
Knab, Frederick	1865–1918	Entomologist.	L. O. Howard.
Kneeland, Samuel	1821–1888	Physician, zoologist.	John F. Fulton.
Knowlton, Frank Hall ..	1860–1926	Paleontologist, botanist.	W. L. Jepson.
Kraemer, Henry	1868–1924	Botanist, pharmacognosist.	Andrew G. Du Mez.
Kuhn, Adam	1741–1817	Physician, botanist.	W. L. Jepson.
Kunze, Richard Ernest ..	1838–1919	Physician, naturalist.	W. L. Jepson.
Langford, Nathaniel Pitt	1832–1911	Vigilante, explorer, first superintendent of Yellowstone National Park.	J. F. Fulton.
Lapham, Increase Allen .	1811–1875	First Wisconsin scientist, [geologist].	Louise P. Kellogg.
Lawrence, George Newbold	1806–1895	Ornithologist, wholesale druggist.	Witmer Stone.
Lawson, John	? –1711	Traveler, author.	Wm. K. Boyd.
Lea, Isaac	1792–1886	Malacologist, publisher.	Wm. B. Marshall.
LeConte, John	1818–1891	Scientist, teacher.	W. W. Kemp.
LeConte, John Lawrence	1825–1883	Entomologist, physician.	L. O. Howard.
LeConte, Joseph	1823–1901	Geologist, [teacher].	G. P. Merrill.
Lederer, John ......fl.	1669–1670	Traveler, explorer.	F. W. Shipman.
Lee, Charles Alfred ...	1801–1872	Physician, scientist.	Edward Preble.
Leidy, Joseph	1823–1891	Naturalist.	G. P. Merrill.
Lemmon, John Gill	1832–1908	Botanist.	W. L. Jepson.
Lesquereux, Leo	1806–1889	Paleobotanist.	G. P. Merrill.
Lesueur, Charles Alexandre	1778–1846	Artist, naturalist, [ichthyologist].	D. S. Jordan.

Name	Dates	Designation	Biographer
Lincecum, Gideon	1793–1874	Frontier physician, naturalist.	S. W. Geiser.
Lindheimer, Ferdinand Jacob	1801–1879	Botanist.	S. W. Geiser.
Lintner, Joseph Albert	1822–1898	Entomologist.	L. O. Howard.
Locke, John	1792–1856	Physician, scientist, inventor, [botanist].	C. W. Mitman.
Locy, William Albert	1857–1924	Zoologist, teacher, historian of the development of biological science.	C. B. Atwell.
Lucas, Frederic Augustus	1852–1929	Naturalist, museum administrator.	Walter Granger.
Lyman, Theodore	1833–1897	Zoologist.	H. M. Varrell.
McGee, William John	1853–1912	Geologist, anthropologist, hydrologist.	Walter Hough.
McLellan, Isaac	1806–1899	Poet, sportsman.	A. L. Bouton, F. E. Bowman.
Maclure, William	1763–1840	Pioneer geologist, patron of science and education, [naturalist].	G. P. Merrill.
McMahon, Bernard	? –1816	Horticulturist, [botanist].	R. H. Sudds.
Marcou, Jules	1824–1898	Geologist.	H. L. Clark.
Marsh, Othniel Charles	1831–1899	Paleontologist.	G. P. Merrill.
Marshall, Humphry	1722–1801	Botanist.	M. P. Smith.
Martin, Henry Newell	1848–1896	Physiologist, [teacher], [biologist].	R. H. Chittenden.
Mather, Fred	1833–1900	Pisciculturist, writer on outdoor life.	M. C. James.
Mather, Stephen Tyng	1867–1930	Organizer and director of National Park Service.	R. S. Yard.
Matthew, William Diller	1871–1930	Vertebrate paleontologist.	Walter Granger.
Maynard, Charles Johnson	1845–1929	Taxidermist, naturalist, [ornithologist].	Witmer Stone.
Mayor, Alfred Goldsborough	1868–1922	Biologist.	C. B. Davenport.
Mearns, Edgar Alexander	1856–1916	Naturalist, army surgeon.	G. S. Miller.
Meehan, Thomas	1826–1901	Botanist, horticulturist, author.	J. W. Harshberger.
Meek, Fielding Bradford	1817–1876	Paleontologist.	G. P. Merrill.
Mell, Patrick Hues	1850–1918	Scientist, educator, [geologist], [botanist].	E. W. Sikes.
Melsheimer, Friedrich Valentin	1749–1814	Lutheran clergyman, entomologist.	G. H. Genzmer.
Merrill, George Perkins	1854–1929	Geologist.	Charles Schuchert.
Merrill, James Cushing	1853–1902	Army surgeon, ornithologist.	J. M. Phalen.
Metcalfe, Samuel Lytler	1798–1856	Chemist, physician, [naturalist].	L. C. Newell.
Michaux, André	1746–1802	Explorer, silviculturist, botanist.	H. B. Baker.
Michaux, François André	1770–1855	Silviculturist, traveler, botanist.	H. B. Baker.
Michener, Ezra	1794–1887	Physician, botanist.	F. Estelle Wells.
Miles, Manly	1826–1898	Agriculturist, naturalist, physician.	R. P. Hibbard.
Miller, Harriet Mann (Olive Thorne Miller)	1831–1918	Author, naturalist.	Sarah G. Bowerman.
Millspaugh, Charles Frederick	1854–1923	Botanist.	C. J. Chamberlain.
Minot, Charles Sedgwick	1852–1914	Biologist, educator.	F. T. Lewis.
Mitchell, Elisha	1793–1857	Geologist, botanist.	Collier Cobb.
Mitchell, John	? –1768	Physician, botanist, author, maker of one map.	Lawrence Martin.
Mohr, Charles Theodore	1824–1901	Botanist.	S. W. Geiser.
Montgomery, Thomas Harrison	1873–1912	Zoologist, teacher.	H. B. Baker.
Morgan, Lewis Henry	1818–1881	Ethnologist, [naturalist].	F. W. Hodge.
Morse, Edward Sylvester	1838–1925	Zoologist, museum director.	F. W. Coburn.
Morton, Samuel George.	1799–1851	Physician, naturalist.	Daniel M. Fisk.
Morton, Thomas	fl. 1622–1647	Adventurer, [outdoorsman].	J. T. Adams.
Mühlenberg, Gotthilf Henry Ernest	1753–1815	Lutheran clergyman, botanist.	G. H. Genzmer.
Muir, John	1838–1914	Naturalist, explorer.	Wm. F. Badè.
Munson, Thomas Volney	1843–1913	Viticulturist, horticulturist, [botanist].	S. W. Geiser.

Name	Dates	Designation	Biographer
Nehrling, Henry	1853–1929	Ornithologist, horticulturist.	Witmer Stone.
Nelson, Julius	1858–1916	Biologist, specialist in oyster culture.	C. R. Woodward.
Newberry, John Strong	1822–1892	Geologist, paleontologist.	G. P. Merrill.
Nuttall, Thomas	1786–1859	Botanist, ornithologist.	Witmer Stone.
Nutting, Charles Cleveland	1858–1927	Ornithologist, marine zoologist.	H. F. Wickham.
Ober, Frederick Albion	1849–1913	Ornithologist.	Herbert Friedmann.
Ord, George	1781–1866	Naturalist, philologist, [ornithologist].	Witmer Stone.
Orton, Edward Francis Baxter	1829–1899	Geologist, educator, [naturalist].	G. P. Merrill.
Orton, James	1830–1877	Zoologist, explorer, educator.	A. L. Treadwell.
Osten Sacken, Carl Robert Romanovich von der	1828–1906	Entomologist, diplomat.	L. O. Howard.
Owen, David Dale	1807–1860	Geologist.	G. P. Merrill.
Packard, Alpheus Spring, Jr.	1839–1905	Entomologist, teacher.	L. O. Howard.
Paine, John Alsop	1840–1912	Archeologist, botanist.	W. F. Albright.
Pammel, Louis Hermann	1862–1931	Botanist, conservationist.	R. I. Cratty.
Parry, Charles Christopher	1823–1890	Botanist.	W. L. Jepson.
Patten, William	1861–1932	Zoologist, paleontologist.	J. H. Gerould.
Pavy, Octave	1844–1884	Arctic explorer, physician, naturalist.	H. A. Marmer.
Peale, Charles Willson	1741–1827	Portrait painter, naturalist, patriot.	H. W. Sellers.
Peale, Titian Ramsay	1799–1885	Naturalist, artist, mathematician, [entomologist].	H. W. Sellers.
Peck, Charles Horton	1833–1917	Mycologist.	W. R. Maxon.
Peck, William Dandridge	1763–1822	Naturalist.	L. O. Howard.
Peckham, George Williams	1845–1914	Teacher, librarian, entomologist.	L. O. Howard.
Perkins, George Henry	1844–1933	Geologist, educator, administrator, [naturalist].	H. L. Fairchild.
Pickering, Charles	1805–1878	Physician, naturalist.	F. Estelle Wells.
Piper, Charles Vancouver	1867–1926	Agronomist, [botanist].	Lee Garby.
Pitcher, Zina	1797–1872	Physician, naturalist.	J. M. Phalen.
Pond, Frederick Eugene ["Will Wildwood"]	1856–1925	Writer on field sports.	G. H. Genzmer.
Porcher, Francis Peyre	1825–1895	Physician, botanist.	Arney R. Childs.
Porter, Thomas Conrad	1822–1901	Botanist.	B. W. Kunkel.
Post, George Edward	1838–1909	Physician, missionary, [botanist].	W. L. Wright, Jr.
Pourtalès, Louis François de	1823–1880	Marine zoologist.	H. L. Clark.
Powell, John Wesley	1834–1902	Geologist, philosopher, administrator, [ethnologist].	G. P. Merrill.
Prince, William	1766–1842	Nurseryman, [botanist].	R. H. Sudds.
Prince, William Robert	1795–1869	Nurseryman, writer on horticultural subjects, [botanist].	R. H. Sudds.
Pringle, Cyrus Guernsey	1838–1911	Plant breeder, collector, [botanist].	Paul D. Evans.
Prosser, Charles Smith	1860–1916	Educator, geologist, [paleobotanist].	J. E. Carman.
Pumpelly, Raphael	1837–1923	Geologist, explorer.	G. P. Merrill.
Pursh, Frederick	1774–1820	Botanist, horticulturist, explorer.	W. R. Maxon.
Putnam, Frederic Ward	1839–1915	Archeologist, naturalist, museum administrator.	R. B. Dixon.
Rafinesque, Constantine Samuel	1783–1840	Naturalist.	G. H. Genzmer.
Rathbun, Richard	1852–1918	Zoologist, museum official.	Marcus Benjamin.
Ravenel, Henry William	1814–1887	Botanist, agricultural writer.	A. R. Childs.
Rice, William North	1845–1928	Geologist, educator.	W. G. Foye.
Richmond, Charles Wallace	1868–1932	Ornithologist.	Herbert Friedmann.
Riddell, John Leonard	1807–1865	Physician, botanist, inventor.	Rudolph Matas, Virginia Gray.
Ridgway, Robert	1850–1929	Ornithologist.	Witmer Stone.
Riley, Charles Valentine	1843–1895	Entomologist.	L. O. Howard.
Roemer, Karl Ferdinand	1818–1891	German geologist, [paleontologist].	F. W. Simonds.

Name	Dates	Designation	Biographer
Rogers, Henry Darwin ..	1808–1866	Geologist, educator, [naturalist].	G. P. Merrill.
Rogers, William Barton.	1804–1882	Geologist, educator, [naturalist].	G. P. Merrill.
Romans, Bernard	1720–1784	Civil engineer, naturalist, cartographer, author, captain of artillery.	W. H. Seibert.
Roosevelt, Robert Barnwell	1829–1906	Political reformer, writer, conservationist.	E. C. Smith.
Roosevelt, Theodore	1858–1919	26th president of the United States, [naturalist].	F. L. Paxson.
Rose, Joseph Nelson ...	1862–1928	Botanist.	W. R. Maxon.
Rothrock, Joseph Trimble	1839–1922	Physician, botanist, forester.	M. P. Smith.
Russell, Israel Cook	1852–1906	Geologist, [geographer], [teacher].	W. H. Hobbs.
Rydberg, Per Axel	1860–1931	Botanist.	J. H. Barnhart.
Safford, James Merrill ..	1822–1907	Geologist, educator.	G. P. Merrill.
Safford, William Edwin .	1859–1926	Botanist, ethnologist, philologist.	W. R. Maxon.
Salisbury, Rollin D. ...	1858–1922	Geologist, educator.	G. P. Merrill.
Samuels, Edward Augustus	1836–1908	Ornithologist, nature lover, sportsman.	H. L. Clark.
Sargent, Charles Sprague	1841–1927	Arboriculturist, [botanist].	John G. Jack.
Sartwell, Henry Parker .	1792–1867	Physician, botanist.	C. W. Dodge.
Saugrain de Vigni, Antoine François	1763–1820	Naturalist, physician, scientist, philosopher.	Stella M. Drumm.
Say, Thomas	1787–1834	Entomologist, conchologist, [naturalist].	L. O. Howard.
Schneider, Albert	1863–1928	Bacteriologist, [botanist], [pharmacologist].	Frederick Grill.
Schöpf, Johann David ..	1752–1800	Physician, scientist, traveler, [naturalist].	G. H. Genzmer.
Schwarz, Eugene Amandus	1844–1928	Entomologist.	L. O. Howard.
Scudder, Samuel Hubbard	1837–1911	Entomologist, [nomenclator].	L. O. Howard.
Sedgwick, William Thompson	1855–1921	Biologist, teacher, epidemiologist.	J. A. Fobey.
Sennett, George Burritt .	1840–1900	Ornithologist.	Herbert Friedmann.
Shaler, Nathaniel Southgate	1841–1906	Geologist, educator, [naturalist].	G. P. Merrill, Eleanor R. Dobson.
Sharp, Dallas Lore	1870–1929	Author, educator, naturalist.	Sidney Gunn.
Shecut, John Linnaeus Edward Whitridge ...	1770–1836	Physician, author, botanist.	A. R. Childs.
Shields, George Oliver ..	1846–1925	Editor, author, pioneer in conservation of wildlife.	Elizabeth W. Heilman.
Silliman, Benjamin	1779–1864	Professor of chemistry and natural history, [geologist].	C. H. Warren.
Smith, Erwin Frink	1854–1927	Botanist, bacteriologist.	J. A. Stevenson.
Smith, James Perrin ...	1864–1931	Paleontologist, geologist.	Solon Shedd.
Smith, John Bernhard ..	1858–1912	Entomologist.	L. O. Howard.
Snow, Francis Huntington	1840–1908	Naturalist, educator, [entomologist].	L. O. Howard.
Spalding, Volney Morgan	1849–1918	Botanist.	W. R. Maxon
Springer, Frank	1848–1927	Lawyer, paleontologist.	G. P. Merrill.
Stearns, Robert Edwards Carter	1827–1909	Naturalist, [conchologist].	S. S. Berry.
Stevenson, John James .	1841–1924	Geologist, [teacher].	G. P. Merrill.
Stimpson, William	1832–1872	Naturalist, [conchologist].	F. C. Baker.
Storer, David Humphreys	1804–1891	Obstetrician, naturalist.	H. R. Viets.
Sullivan, Louis Robert ..	1892–1925	Physical anthropologist, [biologist].	Clark Wissler.
Sullivant, William Starling	1803–1873	Botanist, bryologist.	W. R. Maxon.
Swallow, George Clinton.	1817–1899	Geologist, [botanist].	G. P. Merrill.
Taylor, Charlotte de Bernier	1806–1861	Entomologist, [naturalist].	R. H. Shryock.
Thaxter, Celia	1835–1894	Poet, [nature writer].	G. F. Whicher.
Thaxter, Roland	1858–1932	Botanist.	W. H. Weston, Jr.
Thayer, Abbott Handerson	1849–1921	Painter, ["protective colorationist"].	W. S. Rusk.

Name	Dates	Designation	Biographer
Thomas, Cyrus	1825–1910	Ethnologist, entomologist.	Walter Hough.
Thompson, James Maurice	1844–1901	Poet, author, [naturalist].	F. H. Ristine.
Thompson, Zadock	1796–1856	Historian, naturalist, mathematician.	H. F. Perkins.
Thoreau, Henry David ..	1817–1862	Essayist, poet, transcendentalist, [naturalist].	R. W. Adams, H. S. Canby.
Thurber, George	1821–1890	Botanist, horticulturist, author, editor.	C. R. Woodward.
Titcomb, John Wheelock.	1860–1932	Fish culturist, conservationist.	M. C. James.
Torrey, Bradford	1843–1912	Ornithologist, author.	H. S. Chapman.
Torrey, John	1796–1873	Botanist, chemist.	J. H. Barnhart.
Toumey, James William.	1865–1932	Forester, teacher, [botanist].	H. S. Graves.
Townsend, John Kirk ...	1809–1851	Ornithologist.	Witmer Stone.
Troost, Gerard	1776–1850	Geologist, [naturalist, chemist].	L. C. Glenn.
True, Frederick William.	1858–1914	Zoologist, [mammalogist].	Alexander Wetmore.
Tryon, George Washington	1838–1888	Conchologist.	F. C. Baker.
Tuckerman, Edward	1817–1886	Botanist, authority on lichens.	W. R. Maxon.
Tuckerman, Frederick ..	1857–1929	Comparative anatomist, naturalist.	Henry R. Viets.
Uhler, Philip Reese	1835–1913	Entomologist, librarian.	L. O. Howard.
Underwood, Lucien Marcus	1853–1907	Botanist.	W. R. Maxon.
Van Fleet, Walter	1857–1922	Horticulturist, physician, [naturalist].	W. A. Taylor.
Van Hise, Charles Richard	1857–1918	Geologist, university president, publicist, [conservationist].	G. P. Merrill.
Vasey, George	1822–1893	Botanist.	W. R. Maxon.
Verrill, Addison Emery .	1839–1926	Zoologist	Wesley R. Coe.
Wachsmuth, Charles	1829–1896	Paleontologist.	Charles R. Keyes.
Walcott, Charles Doolittle	1850–1927	Paleontologist, administrator.	G. P. Merrill.
Walsh, Benjamin Dann .	1808–1869	Entomologist.	L. O. Howard.
Ward, Henry Augustus..	1834–1906	Naturalist.	Walter Granger.
Warder, John Aston	1812–1883	Physician, horticulturist, forester, [botanist].	R. H. Anderson.
Warthin, Alfred Scott ..	1866–1931	Physician, educator, [biologist].	Peyton Rous.
Watson, Sereno	1826–1892	Botanist.	B. L. Robinson.
Wayne, Arthur Trezevant	1863–1930	Ornithologist.	Anne K. Gregorie.
Webber, Charles Wilkins.	1819–1856	Author, journalist, explorer, naturalist, soldier.	H. S. Robinson.
Wheeler, George Montague	1842–1905	Topographical engineer, [in charge of "Wheeler" surveys].	T. M. Spaulding.
White, Charles Abiathar.	1826–1910	Geologist, paleontologist, naturalist, physician.	T. W. Stanton.
Whitfield, Robert Parr ..	1828–1910	Paleontologist.	C. A. Reeds.
Whitman, Charles Otis ..	1842–1910	Biologist.	F. R. Lillie.
Whitney, Josiah Dwight .	1819–1896	Geologist, chemist.	G. P. Merrill.
Wilder, Harris Hawthorne	1864–1928	Zoologist.	H. M. Parshley.
Williams, Henry Shaler .	1847–1918	Paleontologist.	G. D. Harris.
Williston, Samuel Wendell	1852–1918	Paleontologist, dipterist.	Ermine C. Case.
Wilson, Alexander	1766–1813	Ornithologist.	Witmer Stone.
Wilson, Ernest Henry ...	1876–1930	Plant collector, botanist.	John G. Jack.
Winchell, Alexander	1824–1891	Author, teacher, geologist, [naturalist].	G. P. Merrill.
Winchell, Newton Horace	1839–1914	Geologist, archeologist, [naturalist].	G. P. Merrill.
Wood, William ......fl.	1629–1635	Author.	K. B. Murdock.
Woodworth, Jay Backus .	1865–1925	Geologist, [teacher].	R. A. Daly.
Worthen, Amos Henry ..	1813–1888	Geologist, [paleontologist].	Carey Croneis.
Wright, Charles	1811–1885	Botanical explorer.	S. W. Geiser.
Wright, George Frederick	1838–1921	Geologist, clergyman, [teacher].	Kemper Fullerton.
Xántus, János	1825–1894	Ornithologist.	Charles Feleky.
Yandell, Lunsford Pitts..	1805–1878	Paleontologist, physician.	J. M. Phalen.
Young, Aaron	1819–1898	Physician, botanist.	Henry R. Viets.

SCYLLA, CHARYBDIS AND DARWIN[1]

DR. CARL EPLING

UNIVERSITY OF CALIFORNIA

IN a brilliant and stimulating paper which was read during the course of a recent symposium upon supraspecific variation, the following statement was made (in flowering plants) that[2]: "We can state categorically that changes in emphasis are of specific rank, while differentiation separates categories higher than species." Such an observation, if of general application, would indeed be of profound importance to systematists. The present writer accordingly sought to apply it to the family of flowering plants with which he is familiar, the *Labiatae*. The results did not bear out the statement.

I. AN EXAMINATION OF GENERIC CHARACTERISTICS IN CERTAIN LABIATAE

In the paper referred to only three examples were cited by name, although other groups of flowering plants were examined: *Aquilegia, Narcissus* (and *Cooperia*) and *Prestonia*. In the first case, the genus *Aquilegia* was viewed as being differentiated from its allies by the presence of the honey petals. The species of *Aquilegia*, however, were viewed as being distinguished from each other by a change

[1] The gist of the present paper formed the basis for remarks at the conclusion of a symposium on the "Concept of the Genus" held at a meeting of the Systematic Section of the Botanical Society of America, the American Association for the Advancement of Science, at Indianapolis, December 29, 1937. The author must acknowledge his indebtedness to Professor Anderson, who kindly discussed the paper with him both before and after its preparation, as well as to his colleague, Professor Hugh Miller.

[2] E. Anderson. A paper read at a Symposium of the American Society of Naturalists in joint session with the American Society of Zoologists, the Botanical Society of America, the Genetics Society of America, the American Phytopathological Society and the Ecological Society of America, the American Association for the Advancement of Science, Atlantic City, New Jersey, December 30, 1936. Later published in the AMERICAN NATURALIST, 71: 223–235, 1937.

in emphasis in pattern of the nectaries or honey petals. That is, the production of the honey petals themselves, characteristic of the whole genus, was interpreted as a fundamental change of pattern, while the specific variations were viewed as changes within the pattern. In similar fashion, the corona of *Narcissus,* contrasted with its absence in the related genus *Cooperia,* was interpreted as a fundamental change of pattern, that is, differentiation. The similar differentiation of *Prestonia* into two species-groups was illustrated by a drawing.

In the genera of *Labiatae* few such striking and simple differentiations as those advanced by Anderson are evident. The nectaries are seldom marked by any elaboration of the corolla tube but are usually set off, if at all, by a patch or ring of hairs. Such patches or rings are not distinctive of genera even in the sense of species-groups and are not in themselves clearly defined but in related species, as in *Hedeoma* (Epling, 1938), may become so diffuse as to lose their identity. It is true, however, that in a few cases the nectary may be marked either by a protuberance outward, to form an inconspicuous sac, as in some parts of *Stachys* (Epling, 1934) or (as in some parts of *Salvia: Calosphace*) may become invaginated to form one or more protuberances inward. In both genera such invaginations or protuberances are usually characteristic of species-groups, as judged upon other grounds as well, except in so far as the species-groups may have become complicated by hybridization past or present.

There are even fewer structures in the *Labiatae* which appear to be of the same order as the corona of *Narcissus.* Two examples may be mentioned, although others might possibly be advanced. Within the genus *Hyptis* (Epling, 1937) supernumerary appendages in the nature of membranous flaps between the calyx teeth appear at two points: within the section *Malvastra,* where they characterize *H. duplicato-dentata,* and within the section *Leptostachys,* where they characterize each of the three species of the

section. The two sections are not otherwise similar. In the first instance, this change in pattern, this addition of something new, is specific and is not found in the other species, which are so closely similar in other respects as to make identification uncertain. In the second it is or has become generic, at least to three species. The supernumerary teeth of *Marrubium vulgare* might also be mentioned as perhaps similar to the first instance. The second example is to be found also within *Hyptis*. In most of the sections of this genus (of which there are approximately thirty) the calyx teeth are linear or subulate, that is to say, narrowed upward. This condition is predominant within the family. Only in the section *Cyanocephalus* do they become enlarged above and more or less clavate. While such teeth are characteristic of this section, they are by no means the sole distinguishing character. A similar condition, which is probably related, exists in the genus *Peltodon* (Epling, 1937). In this genus (of six species) the calyx teeth become expanded at the apex to form a peltate tip. It would appear from gross morphology that the developmental processes involved are scarcely different from those which produce the clavate teeth of *Cyanocephalus*. While it is true that *Peltodon* has been maintained as a genus, it has been maintained primarily on the grounds of expediency and usage. Taxonomically it is no more than a section of *Hyptis,* coordinate with the other sections. This illustrates a point which will be referred to later. In any case might not these differences be viewed as changes in emphasis of the developmental pattern, each of which changes has become congeneric to several species?

In addition to these two examples there are two others of a somewhat different order which might be mentioned. First, there is that of pubescence. There are several types of pubescence to be found within the *Labiatae*, and, while it is true that one type frequently may characterize a species-group or even a genus of several such groups, as in *Lepechinia* (Epling, 1937), nevertheless, I have found

that minutiae of pubescence are, on the whole, most valuable indicators of species. The differences which exist between the pubescence of closely allied species is frequently of a different order or pattern, not merely in the nature of a change in emphasis. For example: in the species-group *Jepsonia* of *Salvia: Audibertia* (Epling, 1938), a single species, *S. leucophylla,* is characterized by branched rather than simple hairs. These hairs seem certainly of a different order of development than the simple often glandular hairs of the remaining species. A second example is the localized development of a portion of the corolla or calyx, such as the tube. The position of the stamens upon the tube of the corolla is such as to suggest that frequently it may have become elongated, either below or above the point of attachment of the stamens. In this way a corolla of somewhat different proportions is produced. If my interpretation is correct, here would seem to be an instance of the localized appearance of change which is commented upon by Professor Anderson. Such changes are variable in degree and may frequently be specific in nature (*Hedeoma, Agastache*), although they may sometimes be characteristic of species-groups, as in *Rubescentes* of *Salvia: Calosphace* (Epling, 1938), or of large genera (calyces of *Hyptis* and *Lepechinia*).

Furthermore, it is very difficult, if at all possible, to distinguish between "change of emphasis" and "differentiation." As an example may be cited the well-known squama or scutellum of *Scutellaria*. At first sight here indeed is an organ which would suggest a fundamental change in pattern. But if the numerous species be arranged in the order of development of the scutellum it will become quickly apparent that there is merely a change of emphasis in the degree to which the upper lip is arched, passing from a shallow inverted bowl, as in *S. Perilomia,* scarcely more pronounced than in some species of *Salvia,* to the erect compressed squama of *S. Brittonii.* The fundamental change in pattern would seem to lie rather in the complete union of the sepals to form the lips.

In a few words, then, after a canvass of the genera of *Labiatae* and an examination of the characters which suggest an origin similar to the examples cited by Professor Anderson, I find that the few which appear are at least as characteristic of species as of species-groups or genera. While it is true that occasional changes in pattern appear, such as he suggests, nevertheless they are by no means so fundamental in significance. They are not characteristic of any single supra-specific category. While it is true that such developmental changes might offer a greater obstruction upon which the factors of isolation might operate and while it is true that such changes might eventually characterize some genera, nevertheless it seems to me clear that in origin they are subspecific and would of necessity have to be submitted to the impact of the various factors which direct evolutionary change. They might or might not become generic in significance, depending upon the particular course of that historical process.

In the *Labiatae,* as understood by me, as well, doubtless, as in other families, the categories higher than species are characterized, just as the species themselves, not by a change in pattern, necessarily, but by different combinations of changes in emphasis. Such combinations in reality produce new patterns. If, for the sake of illustration, species-groups be considered as generic, this fact may be demonstrated by comparison of any of the sections of *Hyptis.* The species-groups, as I have dealt with them in the *Labiatae,* are not improbably of the same order as Turesson's coenospecies.

The genus *Hyptis* (Epling, 1937) is what would be termed by many botanists a natural group. As at present constituted, it consists of something less than 250 species, which range from the Colorado Desert of California and Arizona to Argentina. They are concentrated in the Brazilian Highlands. In corolla and stamens and the interrelationship of these the genus is quite constant. The gynoecium, however, is more variable than in any similar

HYPTIS

TRICHOSPHAERIA   ERIOSPHAERIA   LEPTOSTACHYS

POLYDESMIA   MINTHIDIUM   PUSILLAE

CYANOCEPHALUS   MYRIOCEPHALA   LEUCOCEPHALA
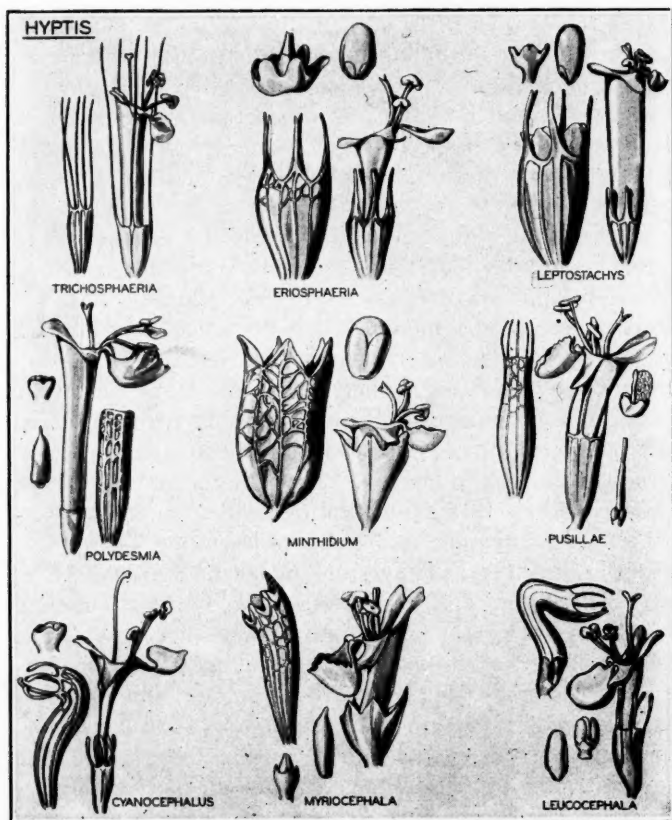
EXPLANATION OF PLATE I

The calyces of *Hyptis* together with the nature of the gynobase, nutlets and general habit offer the most obvious and convenient grounds for segregation into species-groups or sections. The genus as a whole is characterized, amongst other things, by a calyx, which, while commonly turbinate and thin-walled in anthesis, with a tube not greatly different in length from the length of the calyx teeth, becomes elongated at maturity, chiefly below the middle. The calyx teeth do not increase materially nor the upper part of the tube. (Such a habit is also found in other genera as in *Lepechinia*). The calyx teeth vary in shape and texture from deltoid membranous flaps as in *Minthidium* to pungent and rigid spines as in *Eriosphaeria* or aristae in *Trichosphaeria*. They are suppressed in some species of *Polydesmia*. They are clavate in *Cyanocephalus*. They represent all degrees of a ''change in em-

group within the family, particularly in three respects: the conformation of the gynobase and its relation to the style, the degree of coalescence of the style branches and the conformation and outer coat of the nutlets.   The calyx, however, is especially variable, although in the writer's opinion, the variation is one of change of emphasis; the fundamental pattern is scarcely changed.   In habit and inflorescence there is appreciable variation, although most of the species are recognizable as *Hyptis* on the basis of habit minutiae alone.

The genus was first organized by Bentham, and in spite of the not inconsiderable increment of species since his time, the genus stands essentially as he left it.   As it seems to the writer, the species arrange themselves into twenty-seven species-groups, termed sections.   These sections (species-groups) are composed of one to several species which for the most part have expected ("natural") distributions.   The sections, with some exceptions, suggest an origin by fragmentation of some previously existing unit.   They are, in a word, small and "natural" genera. These species-groups are characterized not by the possession of any single organ or trait but rather by an accumulation of differences which might be described as changes in emphasis in the patterns of the several organs mentioned.   These changes in emphasis may be compared by reference to Plate I and the associated explanation.

What has been said regarding the genus *Hyptis* may also be said of *Salvia: Calosphace* (Epling, 1938).   This complex of similar but wider range than *Hyptis* is a natural one, and like *Hyptis* is separable into a series of species-groups (sections), ninety-one in number.   For the most part these species-groups are smaller than in the

phasis,'' and each change is essentially characteristic of one or more species-groups.   But in different species-groups the calyx characteristics occur in different combinations with other similar characteristics.   For example, the calyx of *Myriocephala* has teeth of the same order as those of *Minthidium* but a tube which is flexed as in *Cyanocephalus*, nutlets similar to those of *Polydesmia* and a gynobase more nearly comparable to that of *Eriosphaeria*.

SALVIA CALOSPHACE

SIGMOIDEAE RUDES CYLINDRIFLORAE

MINEATAE PHOENICEAE MITRATAE

MEMBRANACEAE TENUISTACHYA HASTATAE
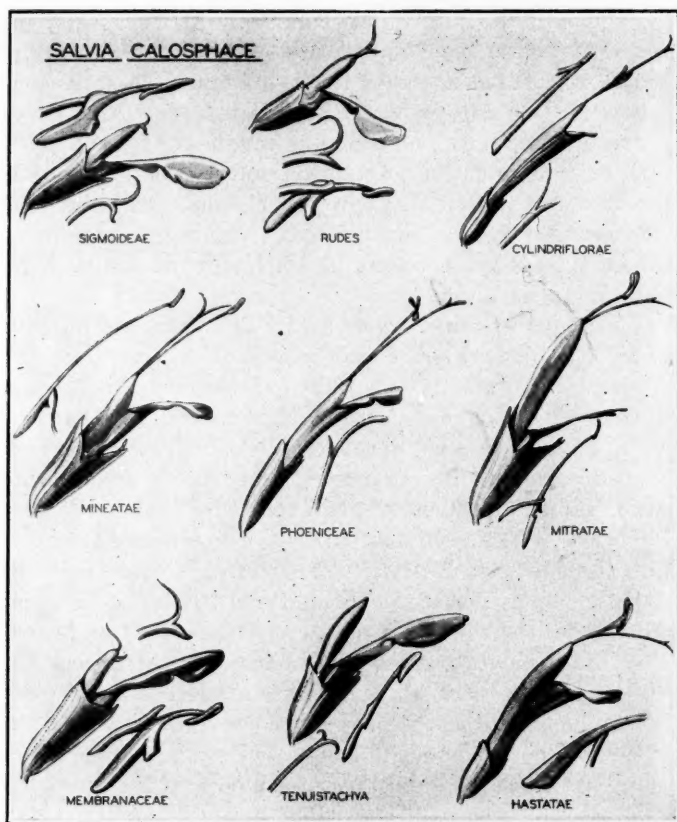
EXPLANATION OF PLATE II

The corollas and stamens of *Hyptis* differ but little throughout the genus and the calyx varies. In *Salvia*, while the calyx varies but little, structure and proportions of the corolla and the relation of the stamens to it are subject to variation and are characteristic of different species-groups. The style branches are also significant, as well as the conformation of the stamens. In comparing *Cylindriflorae*, for example, with *Hastatae*, it is seen that, while both have essentially the same type of stamens and elongated corolla tube, they differ in the nature of the style branches and the proportions of the corolla lips. The same may be said for *Mineatae* and *Mitratae*.

first-named genus, but are characterized by an accumulation of changes in emphasis, particularly in the relation of the stamens to the corolla, the proportion of the corolla lips, the proportion of the style branches and the conformation of the corolla tubes.   These changes in emphasis may be compared by reference to Plate II and the associated explanation.

II. The Concept of the Genus in Relation to Evolution and to System

This attempt of Professor Anderson to find an objective basis for the distinction of species and genera is not the first.   In 1906 Robinson (1906) was saying under somewhat similar circumstances: "What we need in botanical classification is a series of such constants, a number of graded categories which can be generally endorsed and properly respected. . . . Standards as definite as those of the physicist are, of course, unattainable in dealing with the variable and often intergrading groups of organic creation.   But where absolute accuracy and uniformity are impossible, we should the more diligently seek to preserve such standards as exist."

That this attempt has had some degree of success may be seen in the genetic and causal interpretations of species. Nevertheless, it has fostered the idea of the possibility of a *constant* of taxonomic measurement—a modern philosopher's stone.   However, if species and genera are to be treated, not as artifacts, but as segments of an evolutionary pattern it must be recognized that each has its own historical as well as its own genetical background.   It is misleading to assume that a general formula may be found which will apply to all species and all genera.   In other words, evolution is not a unified process but the resultant of the interactions of both genetic and historic processes which operate at different times, at different rates and in different combinations.   Species and genera are accordingly both large and small, both broad and narrow, depending upon the circumstances which have produced them.

However, there is a distinction between species and genera which I believe may be properly advanced, a distinction which serves at the same time to illustrate the essential sameness of species and genera and to suggest that they are segments of one pattern. This distinction may be illustrated by the fact, well known to systematists, that, with an adequate experience within a genus or species-group, it is possible to employ prediction, sometimes upon seemingly tenuous grounds. It is the common experience of those who have had to deal with the floras of little explored places that at some time or other they have described. species from single, frequently fragmentary, specimens. Such predictions of population discontinuity have been repeatedly sustained by subsequent exploration. But it is impossible to predict other species of a genus. The discoverer of *Sequoia sempervirens* could not possibly predict *Sequoia gigantea*. The reason for this distinction lies in the fundamental relationship between the species and the genus.

When viewed in the present time-transect species have reality and may be viewed objectively in the sense that they are segregated interbreeding populations, the individuals of which affect each other in such a way as to preserve the essential integrity of the group. Our concepts of such species are based upon their morphological modes. *In such a context the genus (or species-group) becomes no more than a subjective convenience for the cataloger.* Only when viewed in historical retrospect and not as the compartments of a system, do genera take on reality as the continua into the present of the differentiating processes which once were actual but which are now visible only in their effects. In a word, the genus (apart from its use as a device of classification) is real and significant only to the degree to which it is preserved in the species. *It is an historical phenomenon.*

It is accordingly possible at any time level readily to differentiate between most species, and, as Dobzhansky

(1937) has pointed out, the limits of most species are not subject to debate. In the writer's experience, the debatable cases are confined largely to those instances in which it would seem either that the isolating factors have not yet made effective their impact or that a new synthesis is taking place. But "genera," that is to say, groups of related species, however clearly defined, are still subject to debate and personal preference as to their limits. We are told sometimes that small genera or again that larger genera are more "natural," and as systematists we must therefore make a decision: we must either "maintain" *Salvia* in its present sense or we must segregate its parts to some degree or other. But let it be clearly understood that such a decision confronts the systematist, not the student of evolution. To the student of evolution the genus, the reality, is an historical phenomenon, incapable of measurement and absolute delimitation. To the systematist, the genus is a device of classification and nomenclature, of generalization. Anderson, in the paper discussed above, has suggested a developmental change as a criterion of differentiation of higher categories. That such apparently abrupt changes in pattern occur may hardly be doubted. In the course of evolution it would seem to the writer that they might or might not become generic; it is true, however, that should they become established in several species they might very well serve as the causes for segregation of that particular current as it flowed down the stream of time. In other words, genera form a discontinuous pattern and are grouped about irregularly distributed modes, due presumably to the fact that only a small proportion of the variants possible at one level are realized at the next. The realization of such variants may indeed be a function of differences in pattern as suggested by Anderson.

In classification the two poles of absurdity would be to treat genera either as coextensive with each species or as coextensive with all species. Somewhere between these

poles we must draw our lines, and such lines will be drawn
in part upon personal idiosyncrasy, personal experience
and usage and in part upon the magnitude of the gaps
which the evolutionary process of omissions and commis-
sions may have produced.   It is tempting, at first glance,
to consider the narrow circle of the species-group as the
natural genus: the coenospecies of Turesson.   Here is a
category ·which may be readily defined as consisting of
segregated populations which, when brought together,
would again become integrated.   Such a procedure would
be to define the genus in terms either of potentialities or
in terms of experiment, not in terms of actual existence,
and, as Anderson has pointed out, the limits within which
plants will hybridize are elastic and unpredictable.   Such
a procedure would be to overlook the historical processes
which are in part responsible for the segregation of popu-
lations.   The available evidence suggests to me that, for
example, *Salvia ballotaeflora* of western Texas is closely
allied to *Salvia Gilliesii* of the Argentine Andes and might
very well form a coenospecies with it.   However, the like-
lihood of such widely separated species exchanging genes
at some future time would appear to be remote; it would
seem, rather, that other historical factors would be likely
to intervene first.

Furthermore, the fact must be constantly and clearly
borne in mind by systematists that species-groups have
histories of the same or even greater diversity than the
species which compose them.   Even within closely related
species-groups (judged upon morphological grounds) the
processes of evolution are not necessarily similar and may
be significantly different.   As an example one may revert
to *Salvia*.   *Salvia: Calosphace* may be arranged, as I
have suggested elsewhere, into ninety-one species-groups.
These species-groups (which some systematists might very
properly prefer to consider as genera for purposes of
classification, since they do appear to be the next higher
natural categories) appear to the author to have been

derived, by and large, each by fragmentation of a previously existing species. Such an interpretation is suggested by the morphology and geographic distribution of these groups.   One might cite the species-group *Hastatae,* for example, or *Sigmoideae.* In *Salvia: Audibertia,* on the other hand, a fairly "natural" group has been formed, apparently through hybridization of perhaps three basic forms. The species of this group are relatively diverse, and despite this morphological diversity (of what would often be considered "generic" rank), are interfertile to the extent of forming numerous hybrids. Seemingly a syngameon is either being formed or, having been formed, has begun to fragment.   In this connection it may be said that the occurrence of such constellations within the family has led the author to wonder whether they are the part of an evolutionary rhythm; for the distinctions which characterize the numerous species-groups of *Calosphace* are of essentially the same order as those which characterize the species of *Audibertia.*

This seeming rhythm may be illustrated by reference to an analogous biological phenomenon. The British Empire of post-war years is not the same political organization which was so designated before 1914. Recognition of this change is seen in the term "British Commonwealth of Nations." The change which has taken place is historical, not fundamentally material. A social biologist might perceive in this change the emergence of a generic entity, the specific elements of which may in time become even more isolated and discrete.   Again, in the formation of the Balkan Entente, one might perhaps perceive the beginning of a new synthesis of elements previously detached from each other, a synthesis nevertheless of very different pattern from the older union within the Ottoman Empire.   Such, it seems to the writer, are essentially the processes at work within the *Labiatae.*

Such views of the genus are by no means novel, although apparently not always recognized.   If valid, what impli-

cations do they hold for the systematist? That he recognize, first, that a rigid and doctrinal view of genera is least desirable, whether that view be "broad" or "narrow." It may be necessary to admit that for one purpose or at one time a "conservative" or "broad" view is desirable, for another a more "liberal" or "narrow" one. That he recognize, at the same time, that usage is a factor *in classification* and *nomenclature* which must not be underestimated, however undesirable it may be in the recognition of scientific fact. The individual mind, even though conditioned in some degree, has been unable to keep abreast of the tremendous and rapid increment of specific and generic forms which have been described during the past hundred years. The cementing and coordinating value of many generic names established by wide usage is accordingly an asset.

It is the prescribed function of the systematist to describe the living and present realities in terms of the past. From the outset he is accordingly actuated by dual and conflicting motives. In his portrayal of species he must of necessity stress discontinuities in the present; in his portrayal of genera he must stress continuities with the past. As a classifier he must outline a crystallized and stationary pattern. As a natural historian he must interpret a process of change. A further source of confusion lies in the different approaches and objectives of the floristic and of the monographic writers. Both the floristic writer and monographic writer approach the species with which they deal in essentially the same way. In their approach to genera, however, they frequently differ. The genus is largely a device of classification to the floristic writer. To the monographic writer it is both a device of classification and a means of illuminating the evolutionary processes which have occurred. In the confusion of these facts lie the principal sources of the conflict between the "lumpers" and the "splitters." The title chosen for his paper by Rydberg ("Scylla or Charybdis," 1929) was

revealing, inasmuch as the concepts of species and genera which were employed during the controversy of which that paper formed a part were essentially Scholastic. The dilemma presented by that controversy was sharply etched, but it was not real. The dilemma lay only in the interpretation, not in the reality. The reality as we know it to-day is the dynamic of Darwin.

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CYCLIC CHANGES IN THE THYROID AND ADRENAL CORTEX OF THE MALE STARLING, STURNUS VULGARIS, AND THEIR RELATION TO THE SEXUAL CYCLE[1]

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INTRODUCTION

DUE to the investigations of Bissonnette (1930, 1931), Bissonnette and Chapnick (1930), the normal and experimentally manipulated sexual cycle of the starling is for non-domesticated birds one of the most thoroughly described. The present study is an attempt to learn whether or not the male sexual cycle is accompanied by histological changes in the thyroid and the adrenal cortex.

MATERIALS AND METHODS

Forty-five adult male starlings were collected between November 20, 1936, and June 15, 1937, at about intervals of three weeks (ten collections). Due to the impossibility of securing female birds during the mating and nesting season, the study of this sex was abandoned. Thyroids, suprarenals, testes and reproductive accessories were taken from still-warm birds and fixed in Helly's, Bouin's and Carnoy-LeBrun's (without $HgCl_2$) fluids. Serial sections were made and stained with iron hematoxylin and eosin. In addition, Professor Bissonnette kindly permitted me to section thyroids from some of his starlings which were brought into full spermatogenesis by increased artificial illumination. I wish to thank Mr. E. E. Bailey for his assistance in collecting the birds.

THE SEXUAL CYCLE

In 1936–37 the velocity of the male sexual cycle agreed almost exactly with that described by Bissonnette and

Chapnick (1930), and Bissonnette (1930). During January and February the previously inactive testes slowly increased in size. About March 1 synezesis stages appeared for the first time. By March 22 spermiogenesis had occurred, and spermatozoa were in the epididymides. Spermatogenesis continued in most birds until early June, and as late as June 1 the seminal vesicles contained sperm. However, from mid-May on, there was a noticeable decline in spermatogenesis; the testes decreased in size, and both the epididymides and seminal vesicles showed involution changes. Between June 1 and June 15 a remarkable involution took place. By June 15 the testes became completely devoid of sperm, and the genital duct system had shrunken to almost the resting condition. Hence, the material collected covers (a) the period of testicular inactivity (November to early January), (b) the spermatogenetic cycle (January–May), (c) the early phase of testicular regression (June). Since the starling moults in the summer (Kalmbach and Gabrielson, 1921), the moulting period was not involved in this study.

THE THYROID

1. *Introduction.* Cyclic changes in the avian thyroid have been the subject for a number of studies. Riddle (1925), Riddle and Fisher (1925), using the pigeon, the ring-dove and generic hybrids, find the thyroid increases in size during the fall and winter, and decreases during the spring and summer. The decrease is concomitant with the highest period of reproductive activity. The increase and decrease is considered to be regulated primarily by temperature. Haecker (1926) reports for the carrion-crow a rise in colloid production during the fall with a maximum in the winter. Decrease of colloid occurs during the spring with a minimum in the summer. Küchler (1935, 1935a) has found a more complicated situation in the red-breast, field sparrow, yellow-hammer and house sparrow. In all species, during the year two periods of activity were described; each period consists of an absorp-

tion phase followed by a secretion phase. In the red-breast, the first period falls between late January and the end of April; the second from mid-July to mid-December. For the field sparrow and the yellow-hammer, the active periods are of a shorter duration. The first extends from February to the end of March; the second from the end of July to the end of November. In the house sparrow the first period is covered between mid-April and early July; the second follows immediately and lasts until the end of November. In all birds there is an inactive period at the turn of the year.

2. *Results.* The thyroid of the bird is a paired organ; each portion lies just above the origin of the branchio-cephalic artery. The right portion in the starling is usually larger than the left. In one case the left portion was entirely lacking. It is interesting to note that Haecker (1926) finds in the carrion-crow that the left portion is the larger. In two starlings accessory tissue was noticed lying craniad to the main gland.

When glands for the different dates under study were examined, it became evident that cyclic activity had occurred. In late November and early December the follicular epithelium was a low or flat cuboid. Epithelial cells not organized into follicles (interfollical parenchyma) were scant or lacking. The follicles tended to be of a relatively uniform size,[2] with few very large follicles and with smaller follicles well filled with colloid. Such a gland was clearly one of colloid storage.

Following this period of colloid storage, a phase of very active colloid absorption occurred. The epithelium increased in height to a moderately high cuboid, while its cells became highly vacuolate. The volume of the follicles was greatly reduced, and ultimately the gland was characterized by small, relatively uniformly sized follicles with a very active epithelium. The velocity of colloid

[2] The general use of follicular size for designating various phases of the gland is not to be construed to mean that follicular size is necessarily a diagnostic character for the state of the gland. In this particular instance it simply happened to be a convenient means of designation.

absorption varied with different birds. In some starlings it was obviously under way late in December, and in others it was just beginning by mid-January. However, by late January this process of colloid absorption was generally present.

The end result of this phase was to reduce the gland to one where great areas of parenchymous tissue were present. Follicles in various stages of losing their organization were abundant. In fact, at the very end of this process of disorganization, organized follicles formed a minor portion of the tissue of the gland. This condition was reached in late January and early February.

Following this disorganization came a period of follicular reorganization and colloid secretion which reached a peak during late February and March. This reorganization apparently occurred in an irregular manner. In the early stages a few follicles were very large, while the rest of the gland consisted of various smaller follicles and parenchyma cells. Gradually the follicles became distended with colloid, and large follicles were abundant. However, the parenchyma cells did not all become converted into follicles. There was, moreover, a considerable variation among different birds in the rapidity and also extent of this secretion.

During April and May colloid absorption again occurred. At all times during this period glands characterized by collapsing follicles and great areas of parenchyma tissue were found. The uniform hyperplasia observed in the first period of absorption was not present at this time. Instead, the absorption apparently occurred in a piecemeal fashion, *i.e.*, scattered areas of follicles became active, while other areas remained inactive. Since this absorption phase was superficially the reverse of the previous secretion phase, the whole time from February to May at first glance presented a confused picture, a picture heightened by the individual variations of different birds. However, a closer examination indicated the separation into two phases.

Finally, in late May and June, another period of follicular reorganization and colloid secretion took place. By June 15 the glands were all like those described for November, *i.e.,* characterized by a low follicular epithelium and a relative uniformity of follicular size.

The thyroids from the birds brought into full spermatogenesis by increased illumination all presented a common appearance. The follicles were small, many with little colloid. The cells of the epithelium were broad in width and often approached columnar epithelium in height. These glands were clearly hyperplastic.

3. *Discussion. and Summary.* The thyroids of adult male starlings between November 20 and June 15 histologically showed cyclic behavior. In November and December the glands possessed somewhat uniformly dilated follicles with a low epithelium. No large amounts of parenchyma tissue were present. Such a gland was considered in a colloid storage phase. During January and early February the follicular epithelium increased in height while the follicles became small. The end result of this absorption was to disorganize large areas of the gland into parenchyma tissue (epithelial cells not organized into follicles). In late February and March the follicles were reconstructed again and colloid was secreted. Another loss of colloid then took place in April and May as evidenced most clearly by the general appearance of disorganized glands. During June the thyroid went into a colloid storage phase similar to that found in November. Individual birds varied considerably in regard to the velocity and duration of these changes.

Little correlation can be made from these thyroid cycles with the spermatogenetic cycle. The first period of colloid absorption occurred when spermatogenesis had scarcely begun. In some birds the absorption phase began before spermatogenesis had commenced at all. The second period of absorption roughly corresponded to the mating period. However, the mating season falls after great numbers of spermatozoa have previously been formed.

There was also no agreement between the secretion and storage phases of the gland and spermatogenesis, although the storage phases described as "relatively uniform" were not present during spermatogenesis. In short, there were found no histological changes in non-experimental starlings that could be correlated with the whole sexual cycle. This of course, gives no data on the problem as to whether or not thyroxin is necessary for the sexual cycle. The gland could conceivably secrete enough thyroxin for the spermatogenetic cycle without this secretion being reflected in major changes in the histology of the thyroid.

The whole matter of the relation of the thyroid to the sexual cycle is still obscure. Miller (1935) has reported that thyroxin accelerates the sexual cycle in the house sparrow. Benoit (1936), with the drake, found that thyroxin causes stimulation of the testes, and that thyroidectomy almost abolishes the stimulatory effect of increased illumination. On the other hand, Rowland (1935) thyroidectomized chickens with no resulting check on the sexual cycle.

In the starlings experimentally sexually activated, the hyperplasia of the thyroid may be due to the rapidity and exuberance of spermatogenesis, and may indicate a relation between the thyroid and spermatogenesis. However, the added light which evokes the hypophyseal gonadotropic hormone may also cause increased secretion of the thyrotropic factor. In this latter case the relationship might be merely coincidental.

The Adrenal Cortex

1. *Introduction.* Little is known about cyclic changes in the avian adrenal. Riddle (1923) reported that the whole gland increased in weight during ovulation. The histology of the gland has been described, *e.g.*, Sauer and Latimer (1931) for the chicken.

2. *Results.* As in the reptile, the avian suprarenal shows no segregation of tissues into a cortex surrounding a medulla. Instead, the tissue of the two glands is inter-

mingled; the cortical and medullary tissue occur in an irregular interwoven network of cords which are primarily two cells in thickness. The two tissues are about equally distributed throughout the gland, and there are no zones predominately either cortical or medullary. As Sauer and Latimer suggested for the chicken, there appears to be in the starling a differentiation of the more peripheral cortical cells resembling the *zona glomerulosa* of the mammal.

In the cortex changes occurred coincident with the sexual cycle. During the period of testicular quiescence the cortex consisted of a number of cell types. As in all periods the spongiocytes were the predominant type. Many of these spongiocytes were not fully elaborated, and their cytoplasm was more or less uniform (nonvacuolate). In addition, especially toward the periphery of the gland, there were very large, fat-laden cells whose cytoplasm, because of the large vacuoles, appeared colorless. A third type was a small cell with a scant, darkly staining cytoplasm.

However, from late January to late May, the period of spermatogenesis, the character of the gland changed. In place of a variety of cell types, the cortex consists almost entirely of spongiocytes which show the characteristic delicate, lace-like reticulum in the cytoplasm. The large, fat-laden cells have disappeared, and the small, dark cells are less numerous. Thus the cortex presents a uniform appearance which was characteristic of all birds during this period with one exception. On April 14, at about the height of spermatogenetic activity, two birds with testes normal for this period showed glands with the variety of cell types described for the first period. Other birds collected about this date (April 13 and 15) were of the uniform type.

Beginning with late May until June 15 (after this latter date no birds were collected), which is the period of rapid decline of spermatogenesis and of testicular involution, the cortex again possessed the variety of cell types present in the period, November to January.

Hence, during spermatogenesis the adrenal cortex of the starling assumes a uniform appearance characterized by elaborate spongiocytes. During sexual quiescence and involution other cell types are also present. Only one exception was found: this consisted of glands from two birds on April 14. Here the uniform appearance of the gland was lacking. The significance of this deviation is not known.

Since cyclic changes in the avian cortex have not been generally studied, it is not wise at this time to correlate these results with those reported for mammals. Such a correlation had best be postponed until a variety of birds has been thoroughly investigated.

Summary and Conclusions

(1) Changes in the thyroid and adrenal cortex of the male starling, which occurred between November 20 and June 15, were described in relation to the spermatogenetic cycle. The periods under study included: (a) a period of testicular quiescence (November to early January); (b) the spermatogenetic cycle (January to the end of May); (c) testicular involution (June).

(2) The phases of thyroid activity described were: (a) colloid storage (November and December); (b) colloid absorption (January to early February); (c) colloid secretion (February and March); (d) colloid absorption (April and May); (e) colloid secretion (June). Variations in velocity and duration of these phases were noted.

(3) Starlings brought into full spermatogenesis by increased artificial illumination uniformly showed a hyperplasia of the follicular epithelium. The significance of this finding is discussed.

(4) It is concluded that normal spermatogenesis is accompanied by no histological change in the thyroid that can be correlated with this cycle as a whole. One period of colloid resorption, however, roughly corresponded with the mating period.

(5) Changes in the adrenal cortex can be correlated

with the spermatogenetic cycle. During the period of spermatogenesis the cortex presented a uniform appearance characterized by fully elaborated spongiocytes. During sexual quiescence and sexual involution other cell types also occurred.

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SHORTER ARTICLES AND DISCUSSION

NOTE ON ANOMALOUS INHERITANCE OF SEX–LINKED COLOR FACTORS IN THE GUPPYI

SEVERAL years ago the authors of the present note desired to obtain biological material for a study of the assortment of genetic factors which behave as though located in the Y-chromosome (*i.e.*, are inherited from male to male, irrespective of the female parentage) when the germ cells of the organism are irradiated with fairly heavy dosages of x-rays. It was particularly desired to study the generally little-known phenomenon of crossing-over apparently occurring between the X and Y chromosomes.

The viviparous Poecillid guppyi, *Lebistes reticulatus,* native to Trinidad and the northeast coast of South America and well known to fish fanciers, has proven nearly ideal for this purpose. Numerous races exist which are differentiated on the basis of the color pattern in the brilliantly colored male, and are completely interfertile. Winge[1] has shown in a series of papers that inheritance behaves as though of the XY type in this species, and has located color factors in the Y-chromosome (where most of them appear to lie), the X-chromosome and autosomes. He has reported that his character *Luteus,* phenotypically expressed as heavy yellow pigmentation in the caudal of the male, shows a considerable percentage of crossover normally. The character *Maculatus,* however, phenotypically expressed as an intense black spot in the dorsal of the male and behaving as though located in the Y-chromosome, exhibits a negligible tendency to crossover. This is also true for the factor *Armatus,* expressed in adult males as an elongation and yellow coloration of the lowest rays of the caudal fin to produce a "sword."

We have undertaken a fairly extensive series of studies of such characters under normal conditions as a preliminary to x-ray studies and have over the past five years obtained several inter-

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[1] O. Winge, *Jour. Gen.,* xii, 137; *ibid.,* xii, 145; *ibid.,* xiii, 201; *ibid.,* xviii, 1.

esting results.   Studies with which this note is concerned were
confined entirely to the three sex-linked characters described.
Purebred stocks from fish kindly sent from Copenhagen by Winge
were used, as well as stocks selected from American aquaria and
others obtained directly in Trinidad.   Confirmatory results were
obtained for all three sources.   In general, the phenotypic results
obtained by Winge were observed, with one or two additional
features that seem worth adding.

Two examples will illustrate the nature of results in general
confirmatory.   In the first case a male *Armatus* (*Ar*) was out-
crossed with a female of *Luteus* (*Lu*) stock.   The F_1 generation
showed thirteen males, five of which were normal *Ar*, six *Ar-Lu*
and two neither *Ar* nor *Lu*.   Males of the *Ar-Lu* type were then
backcrossed to females of both *Ar* and *Lu* stocks, and were also
outcrossed to stock of neither type.   The results were uniform.
A representative group of twenty-seven F_2 males showed twenty-
six *Ar* and one questionable *Lu*.

These results can be explained, with reservations, on the as-
sumption of simple crossover from the Y-chromosome.   The two
exceptional fish in the F_1 generation can be conceivably con-
sidered as resultant on a complete gametic elimination of the
Y-chromosome, while the exceptional F_2 case might have been con-
sequent upon a sex reversal in one *Lu*-containing potential female,
such as is known to occur with relatively high frequency in the
guppyi.   The remainder of the males can then logically be ac-
counted for on the assumption of a *Lu* crossover in the original
female parent.

The second case, although apparently rather similar as regards
the F_1 generation, will permit of no such interpretation.   A *Lu*
male was crossed to a female from *Ma* stock.   Eleven males ma-
tured in the F_1 generation.   Six of these were *Lu*, four were *Ma*,
while eleven were *Ma-Lu*.   Males of *Ma-Lu* were then backcrossed
to both *Ma* and *Lu* females.   The results were uniform, indicating
that in the F_1 backcross neither type of female contained the color
factor.   A typical brood of F_2 matured ninety males.   Forty-four
of these were *Ma*, forty-four *Lu* and two *Ma-Lu* like the father.

This situation can be consistently pictured in one of two ways.
It can be interpreted by assuming an attached-Y for the female,

similar to the non-disjunctional cases observed by Aida for *Aplocheilus*,[2] on the further assumption that a fish of constitution XXY in F_1 and F_2 may be male, which is reasonable from what we know of Poecillid inheritance in general.[3] The theoretical F_2 under these conditions will consist of equal numbers of *Ma* and *Lu*, with no *Ma-Lu*, provided chromosome division among gametes in the F_1 *Ma-Lu* male used in the backcross (of constitution XYY) is Y + XY. Should any sex cells so divide as to apportion the chromosomes among gametes as X + YY, only males of constitution *Ma-Lu* would theoretically be expected in F_2. The two *Ma-Lu* individuals observed in the F_2 may have resulted from such a split.

A second explanation may be had from the same phenomenon by assuming that the female in the original stock was actually of XY composition. This phenomenon has been reported by Winge[4] in his *Ma* stock, and is perhaps the preferable interpretation. In this case, the exceptional F_2 males might result on the production of a non-disjunctional, YY gamete. A further study of male-female sex ratios is in progress in this connection.

The color factor *Ma* can be made to exhibit further anomalies in inheritance, as illustrated by the following case.

It was desirable for a number of purposes that autosomally inherited color factors be incorporated into stock containing the standard Y-linked ones. Such factors are not common in the guppyi, but one of the best, *fredlini* (*fr*) leads to a reduction in micromelanophore pigmentation of the scales of the whole body in both sexes, producing a generally golden background coloration. The appearance of the sex-linked colors in the male is not normally inhibited, however, and they are laid down faithfully, although in somewhat reduced intensity, against the lighter background. The character is a simple single-factor recessive, and when introduced into stocks of *Armatus, Luteus* and some five other similarly sex-linked genes, one fourth of the F_2 males showed the typical sex coloration in combination with the autosomal character. This was not the case for stock of *Maculatus*, however, whether derived from Winge's original material or from North

[2] T. Aida, *Genetics*, vi, 554.

[3] O. Winge, *Jour. Gen.*, xxiii, 69; *Proc. 6th Int. Cong. Gen.*, 1 (1932); *C. R. Lab. Carlsberg*, 21.

[4] O. Winge, *C. R. Lab. Carlsberg*, 22.

American or Trinidad sources.   Here only somewhat less than half of the F_2 males showing the *fredlini* character also showed *Ma*.   However, when such *fredlini*, phenotypically non-*Ma* males were outcrossed to non-*fredlini*, non-*Ma* females, all the F_1 males were non-*fredlini*, *Ma* in character.   *Ma* may thus, under certain conditions, be phenotypically absent while genetically present, and some account must be taken of this apparent susceptibility of the character to inhibitors in any picture of *Ma* inheritance.

No comprehensive explanation is attempted for the behavior described.   Work is in progress on the study of sex-ratios, and in the introduction of new factors into the *Lebistes* complex, in the hope of further elucidating the behavior of the *Maculatus* gene.

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THE EFFECT OF TEMPERATURE ON EYE COLOR IN *HABROBRACON JUGLANDIS* (ASHMEAD)[1]

Temperature is an important factor in the development of color among insects.   Piepho (1935) found that two red-eyed strains of the moth *Ephestia*, R_1 and R_2, showed different shades of red eye color when raised at 18°; that both became lighter at 25°, R_2 being modified more than R_1; that if R_1 was changed from 18° to 25° after 60 per cent. of its development was complete, the eye color was the same as if all its development had taken place at 25°; and that the same was true for R_2 when transferred after 45 per cent. of its development.   In a mottled-eyed stock of *Drosophila* (Surrarrer, 1935) the eyes ranged from an almost solid color at 18° to a practically colorless condition at 24° or over.   In the wasp *Habrobracon*, Schlottke (1926) showed that the intensity of body pigment varied inversely with the temperature, the color ranging from black at lower temperature (16°) to a light golden yellow at higher temperature (35°).

When carrot-eyed wasps (wh^c) were reared in a cool room in order to delay development, the writer noticed that the color of the eyes of the emerged wasps was white, phenotypically similar to genotypic white (wh). Offspring from these "white-eyed" wasps reared at 30° developed carrot eyes like their grandparents.

Experiments were then conducted to test the effect of temperature on eye color in the mutant types carrot (wh^c), red (rd) and the combination carrot-red (wh^c · rd), the temperature ranging from around 15° up to 37.2°. The lower temperature was not exact, since it was obtained in a cool cellar room instead of an incubator. Female wasps were placed with fresh *Ephestia* caterpillars and put in an incubator at 29° (Zürich) or 30° (Storrs), and on the third or fourth day the offspring, including eggs and larvae, were transferred to other temperatures. Some were transferred at later stages in order to see when the eye-color was determined.

Among the carrot-eyed wasps the amount of pigment varied directly with the temperature, the eyes ranging from white (black body) at low temperature, through pale yellow, to a typical carrot, and finally to a deep reddish carrot (body very pale yellow) at high temperature. The eye color among the red-eyed wasps did not show such wide variation, but ranged from bright red at low temperature to black or dark red at high temperature. The bright red (rd) and the deep reddish carrot (wh^c) were somewhat similar in appearance. The combination carrot-red was similarly affected; that is, the color ranged from a white through an opalescent white to a distinct though rather pale carrot, with increasing temperature. Of the combinations reported by Whiting (1934), carrot-maroon (wh^c · ma) was white and carrot-dahlia (wh^c · o^d) was a lightened carrot. The extent of likeness between carrot-dahlia and carrot-red reared at the same temperature is unknown.

In linkage studies of carrot and red (30°), pale-eyed individuals were encountered occasionally in which it was impossible to say without a genetic test whether they were carrot or carrot-red. Since the wasps in a single vial are not all the same age, those not yet emerged were exposed to room (lower) temperature while their sibs were being counted, often for 2 to 4 hours, sometimes a day or two. And in some cases these younger wasps were allowed to complete their development at room tem-

perature.   Only later was it learned that the end of development is a crucial period as regards the eye color, and it was found then that if carrot-eyed young are transferred from 30° to room temperature as late as the 7th day of development the eyes are practically colorless.   Body color is determined earlier than eye color and appropriate changes of carrot larvae from higher to lower temperature during development, and *vice versa,* can produce various combinations of light and dark eye and body color.

The body color of wasps with the mutant factor lemon (le) became somewhat darker (sooty lemon) when reared at lower temperature.

Limited experiments with the cantaloup (c) eye color indicate that the intensity of this color, unlike carrot, is affected little, if any, by a lowering of the temperature, although bodies of such wasps showed the usual changes.   (Perhaps it should be stated here that the cantaloup eye color turns to a deep red with an increase in age.)

The time of development at the different temperatures corresponds roughly to that given by Schlottke.   In my experiments the time ranged from 7 days (young transferred on the third day from 30° to 37.2°) to 37 days (young transferred on third day from 30° to cool cellar room).   The results of the lower temperature are very rough, and make no allowance for possible effect of repeated alterations of temperature on the rate of development.

Summary

Carrot (wh^c), red (rd) and carrot-red (wh$^c \cdot$ rd) eye-colors in *Habrobracon* vary directly with temperature, in contrast to body color, which varies inversely.   At 30° the combination carrot-red is a pale yellow.

The eyes of carrot (wh^c) wasps reared at a low temperature are white, phenotypically indistinguishable from genotypic white (wh).   Cantaloup (c) does not respond to changes in temperature, as does carrot.

Body color is determined earlier in development than eye color.   Lemon (le) body color is darkened if the wasps are reared at low temperature.

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ON THE PRODUCTION OF "STERILE" EGGS IN HABROBRACON

In 1922 Hase described three types of eggs—fertilized, unfertilized and "sterile"—that were deposited by mated females of *Habrobracon brevicornis*. The ova showed no external distinguishing characteristics upon deposition, but a short time thereafter a number of them became conspicuous by shrinking, which resulted in their callous or horny appearance. Such eggs, found also among those laid by unmated females, were designated "sterile" because they never developed into larvae. Although Hase made no cytologic examination of these eggs, he believed that their failure to develop was probably due to the decomposition of the ooplasm. "Sterile" ova were obtained by him even under the best nutritive conditions and favorable temperature. In one experiment he observed 188 "sterile" eggs out of 317 that were deposited.

A cause for the production of "sterile" ova in *H. juglandis* was ascertained by the author while collecting eggs (Spotkov, 1938) and studying the behavior of the wasps during oviposition. It was discovered that such eggs were obtained only if they remained after deposition on or under the caterpillar which the wasps continued to use as a source of food and egg depository. On the other hand, no "sterile" ova were ever found after eggs had been removed from the caterpillar upon deposition. The cytologic study of more than 900 eggs which were set aside immediately after oviposition and fixed at ten-minute intervals during the first hour of development revealed only 5 ova that could be considered as abnormal. Whether the latter were capable of developing is unknown. However, this is in remarkable contrast to the number of "sterile" ova obtained by Hase.

Just before the wasp oviposits on the torpid caterpillar, she moves about with her abdomen bent downward and thrust forward so that the sting protrudes beyond the gonapophyses. This behavior enables the finely pointed sting to come into contact with ova which have been laid previously, and puncture them accidentally. In most instances this accidental puncture causes some loss of protoplasm, which results in a visible shrinkage and a callous appearance of eggs. That an upset in development follows is indubitable, since eggs which were punctured with loss of ooplasm in micro-manipulation experiments manifested a definite abnormal ontogeny through the transparent chorion. Furthermore, such eggs resembled the "sterile" ova found on caterpillars.

It is apparent, therefore, that in *H. juglandis* "sterile" ova, as described by Hase, may be produced through the accidental puncture of eggs by the sting during oviposition. This suggests that a similar cause for the production of "sterile" ova in *H. brevicornis* might also be observed.

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